Lake Fertilization and Enhanced Growth of Juvenile Sockeye Salmon at Woss Lake, British Columbia: A Food Web Analysis

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LAKE FERTILIZATION AND ENHANCED GROWTH OF JUVENILE SOCKEYE SALMON AT WOSS LAKE, BRITISH COLUMBIA: A FOOD WEB ANALYSIS

by

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ABSTRACT

Hyatt, K.D., McQueen, D.J., Rankin, P.D., Hanslit, B., Sutey, S., Carey, E., Nelson, H., and Svanvik, B. 2004. Lake fertilization and enhanced growth of juvenile sockeye salmon at Woss Lake, British Columbia: a food web analysis. Can. Manuscr. Rep. Fish. Aquat. Sci. 2689: 169 p.

Our objective was to determine whether whole-lake fertilization (years 2000 - 03) of Woss Lake (Vancouver Island), could reliably increase the production of juvenile sockeye salmon by altering their growth and/or survival. Vernon Lake was maintained as an unfertilized control. Our approach was to quantify changes in the phytoplankton taxa, calculate production and consumption for zooplankton species, calculate growth and production for juvenile sockeye and then to calculate the species-specific consumption rates of sockeye on each of the major zooplankton taxa. We used these data to estimate the proportion of species-specific zooplankton production and standing stock consumed by sockeye. We found that because Woss Lake (fertilized) fish densities were low (<1000 ha^{-1}), juvenile sockeye consumed very little of the available zooplankton and had no density dependent effects on zooplankton biomass. Also because Woss Lake was subject to blooms of *Rhizosolenia,* an algae that is large and ungrazable, <20% of the algal production was available to zooplankton, and < 0.1 % of the fertilizer added to Woss Lake, was incorporated into fish biomass. On the other hand, even that small amount of fertilizer stimulated an additional 3-19 % (depending on year) increase in sockeye production. This translated into 69 kg of additional 0+ sockeye production in 2000, 114 kg in 2001, 399 kg in 2002 and 206 kg in 2003. Given the unused zooplankton production capacity that was generated by fertilization, 0+ sockeye production could have been 2-3 times greater had the fish densities been greater. Recommendations for future sockeye population restoration in Woss Lake include: (1) Resumption of the Woss Lake fertilization program in 2005, using a low N:P ratio fertilizer mix designed to increase primary production while reducing the chances of *Rhizosolenia* blooms, and (2) stocking 2,000,000 sockeye fry from the Gwa'ni Hatchery, in order to take advantage of the anticipated increases in primary production.

RÉSUMÉ

Hyatt, K.D., McQueen, D.J., Rankin, P.D., Hanslit, B., Sutey, S., Carey, E., Nelson, H., and Svanvik, B. 2004. Lake fertilization and enhanced growth of juvenile sockeye salmon at Woss Lake, British Columbia: a food web analysis. Can. Manuscr. Rep. Fish. Aquat. Sci. 2689: 169 p.

Notre objectif était de déterminer si la fertilisation panlacustre (de 2000 à 2003) du lac Woss (île de Vancouver) pouvait de façon fiable faire augmenter la production de saumons rouges juvéniles en modifiant leur taux de croissance et/ou de survie. Le lac Vernon a servi de site témoin non fertilisé. Notre approche consistait à quantifier les modifications survenues dans les taxons phytoplanctoniques, à calculer la production et la consommation des espèces zooplanctoniques, à calculer le taux de croissance et de production des saumons rouges juvéniles, puis à calculer le taux de consommation, spécifique à l'espèce, de chacun des principaux taxons zooplanctoniques par les saumons rouges. À partir de ces données, nous avons estimé la proportion de la production et de la biomasse zooplanctonique (au niveau de l'espèce) consommée par les saumons rouges. Nous avons découvert que, les densités de poissons dans le lac Woss (fertilisé) étant faibles (<1000 ha^{-1}), les saumons rouges juvéniles consommaient une très petite quantité du zooplancton disponible et n'avaient pas d'effets dépendants de la densité sur la biomasse zooplanctonique. En outre, le lac Woss étant soumis à des efflorescences de *Rhizosolenia,* une algue de grande taille qui n'est pas broutable, < 20 % de la production algale était à la disposition du zooplancton, et < 0,1 % de l'engrais s'incorporait à la biomasse ichtyenne. Par ailleurs, même à ce faible niveau, l'apport d'engrais a suscité une augmentation de 3-19 % (selon l'année) de la production de saumons rouges, ce qui s'est traduit par un accroissement de la production de saumons rouges d'âge 0+ de 69 kg en 2000, de 114 kg en 2001, de 399 kg en 2002 et de 206 kg en 2003. Étant donné la capacité de production zooplanctonique inutilisée qui a été générée par la fertilisation, la production de saumons rouges d'âge 0+ aurait pu être 2 à 3 fois plus élevée si les densités de poissons avaient été supérieures. Des recommandations sont présentées pour le rétablissement futur de la population de saumons rouges dans le lac Woss : (1) reprise du programme de fertilisation du lac Woss en 2005, à l'aide d'un engrais à faible rapport N:P visant à accroître la production primaire tout en réduisant les risques d'efflorescence de *Rhizosolenia*, et (2) ensemencement de 2 000 000 d'alevins de saumons rouges provenant de l'écloserie Gwa'ni, afin de tirer parti de l'augmentation prévue de la production primaire.

INTRODUCTION

Almost 50 years ago, Foerster (1968) suggested that observed declines in sockeye salmon populations might be explained in part, by the "smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners". In accordance with this observation, a group of scientists from the Pacific Biological Station at Nanaimo, and the University of British Columbia; began the 1969 enrichment of Great Central Lake, Vancouver Island, BC. This large-scale experiment was based on the assertion (Barraclough and Robinson 1972), that "Decomposing bodies of anadromous fish, such as sockeye salmon (*Oncorhynchus nerka)* contribute to the fertilization of nursery lakes following spawning in the lake." ... "removal of maturing sockeye by the commercial fishery may deny lake waters of their essential nutrients and contribute to lowered productivity". The objective of the Great Central Lake (GCL), experiment was to test the hypothesis that artificial fertilization could replace the sockeye carcasses removed by the commercial fishery. The results after the first year of fertilization (1970) appeared to be very positive (Parsons et al. 1972, LeBrasseur and Kennedy 1972, Barraclough and Robinson 1972). This led to the continued fertilization of GCL, and in 1977, contributed to the establishment of a large-scale Lake Enrichment Program (LEP - sponsored by Canada's Salmonid Enhancement Program), which began with six lakes and grew through the late 1970s, 1980s and early 1990s to include 17 sockeye nursery lakes (Hilborn and Winton 1993). Published results from these studies are summarized in the pages that follow. Extensive nursery lake fertilization work was also ongoing in Alaska. During 1979, the Division of Fisheries Rehabilitation, Enhancement, and Development (FRED), a section of the Alaska Department of Fish and Game, initiated a nutrient enrichment and fry outplanting program that included 16 Lakes (Kyle et al. 1987). Results from these experiments are summarized in the pages that follow. Finally, in more recent times, support to both LEP and FRED has declined, but the potential importance of lake fertilization has been recognized by other government agencies and NGOs, and the work has been extended to include lake fertilizations to enhance kokanee populations in British Columbia (Ashley et al. 1999, Pieters et al. 2002), and a sockeye nursery lake fertilization in Idaho.

FOOD WEB THEORY

Lake fertilization theory is based on two assumptions (Nelson and Edmonson 1955). The first assumption is that the size and survival advantages gained by fry originating from fertilized lakes, can be successfully carried into the marine environment, thus ensuring increased escapement. Ricker (1962) showed that over a broad geographical range, there was a positive relationship between sockeye smolt length and marine survival, and similar relationships have also been demonstrated for sockeye from the Karluk River (Barnaby 1944) and Cultus Lake (Foerster 1954). The question is, do these general patterns apply to sockeye nursery lakes, where artificial fertilization is supposed to increase smolt sizes? The second assumption is that the pelagic zones of lakes are primarily donor-controlled systems, and that substantial portions of the nutrient added at the bottom of the food web will successfully make its way from algae to fish. There is general agreement that decomposing bodies of spawning salmon contribute highly variable, but sometimes substantial fractions (0 – 95% depending on the lake) of the annual nutrient load to sockeye nursery lakes (Willson and Halupka 1995, Bilby et al. 1996, Larkin and Slaney 1997, Cederholm et al. 1989, 1999; Cederholm 2000, Gresh et al. 2000, Thomas et al. 2002). There is also general agreement that these missing nutrients, normally provided through bacterial remineralization of salmon carcasses, can be replaced through lake fertilization (Stockner and MacIsaac 1996). The assumption is that the donor-controlled (bottom-up) trophic transfers between nutrients → algae → zooplankton → fish; are both predictable and strong. Over the past 30 years, the food web literature has verified the general predictability of bottom-up relationships between nutrients and algae (reviewed in Dillon and Rigler 1975, Stockner and Shortreed 1985), algae and zooplankton (reviewed in McCauley and Kalff 1981, Hanson and Peters 1984) and (3) zooplankton and planktivorous fish (reviewed in Downing et al. 1990, Koenings and Kyle 1997). However, during the last 20 years, the same literature has featured considerable disagreement about the relative strength of these bottom-up relations (reviewed in McQueen et al. 1986, 1989), and about the relative importance of top-down processes (Shapiro et al. 1975, Carpenter et al. 1985) which tend to dilute donor-control. In a nutshell, food web theory supports the assertion that overall trophic level biomass is regulated by nutrient availability, but there is considerable uncertainty about the proportion of the energy added in fertilizers, that can successfully move from algae to fish. The question is, can substantial amounts of energy added as fertilizer make its way up the food web causing juvenile sockeye to survive better and grow larger?

Field studies with relatively clear-cut results (Summarized in Table 1).

Leisure Lake - Alaska: Leisure Lake (1.1 km ^{2}) was stocked with about 2 million sockeye salmon fry per year from 1980-85 and then stocked and very heavily fertilized (31100 g N and 3455 g P ha^{-1} y^{-1}) from 1985-92, (Kyle 1994, Koenings and Kyle 1997). Nutrients, chlorophyll and zooplankton were recorded for 1982-84 (unfertilized) and 1985-92 (fertilized). Fertilization produced almost immediate results. Mean annual epilimnetic total phosphorus (TP) increased by 70% (5.3 unfertilized vs. 9.0 µg L^{-1} fertilized) and mean annual chlorophyll a increased by 500 % (0.65 unfertilized vs. 3.65 µg L^{-1} fertilized). Zooplankton biomass increased by > 700 % (mean annual biomass unfertilized 70 vs. 600 mg m^{-2} dw fertilized). Smolt weights increased by 112 % (mean weight unfertilized 1.7 g vs. 3.7 g fertilized), smolt age decreased, and total stocked-fry to smolt survival almost doubled (three year mean annual unfertilized 16% vs. 27 % fertilized) although between-year variability was high and the differences were not significant. Finally, marine survival averaged over three years, also increased (11.4% unfertilized vs. 14.2 % fertilized), but between-year variability was very high (13.8, 6.8, 13.7 % unfertilized vs. 24.4, 9.9, 8.2 % fertilized) and the differences were not significant.

Fraser Lake - Alaska: Fraser Lake (16.6 km^2), was seeded with sockeye eggs in 1951 and during 1964-86, sockeye escapement increased from 14,000 to 257,000

y^{-1} and mean annual smolt lengths and weights decreased from 148 mm to 89 mm and 29.5 g to 5.9 g (Kyle et al. 1988, Kyle 1994, Koenings and Kyle 1997). During 1988-92, Fraser Lake was fertilized (8940 g N and 982 g P ha^{-1} y^{-1}). Data for nutrients, chlorophyll, zooplankton and fish were recorded for 1985-87 (unfertilized) and 1988-92 (fertilized). During the fertilized years, mean annual epilimnetic TP increased by 19% (6.7 unfertilized vs. 8.0 µg L^{-1} fertilized) and mean annual chlorophyll a increased by 37 % (1.00 unfertilized vs. 1.37 µg L^{-1} fertilized). Zooplankton biomass increased by 100 % (mean annual biomass unfertilized 150 vs. 300 mg m^{-2} dw fertilized). Smolt weights increased by 42 % (mean weight unfertilized 3.6 g vs. 5.1 g fertilized). During years when escapement overshot the "escapement goal" based on the EV model (see next section), fall-fry lengths declined and when escapement was below or near the escapement goal, fall-fry lengths remained approximately stable at 65 mm and smolt weights also increased. The authors conclude that within limits, fertilization of Fraser Lake counter-balanced top-down effects on zooplankton, so that stock densities could be increased without obvious density-dependent declines in smolt weights.

Coghill Lake - Alaska: Edmundson et al (1997) described trophic-level responses to the nutrient treatment of Coghill Lake (1270 ha). Escapements into Coghill Lake during 1980-90 were the highest in Prince William Sound. However during 1990-94, the run sizes declined, possibly in response to earlier over-grazing of the zooplankton forage base. The lake was fertilized (3161g N and 812 g P ha^{-1} y^{-1}) during 1993-96, and stocked during 1995-96. The added fertilizer accounted for 40-60% of TP loading (carcasses accounted for about 10%). A comparison of seasonal means for unfertilized years (1988-92) with fertilized years (1993-96) showed that: TP increased (mean annual TP 8.0 unfertilized vs. 9.8 µg L^{-1} fertilized), NO_3 decreased (18.8 unfertilized vs. 13.4 µg L^{-1} fertilized), chlorophyll a increased (mean summer concentration 0.64 unfertilized vs. 2.05 µg L^{-1} fertilized). In response to fertilization, zooplankton biomass (comprising > 90% cyclopoids, some bosminids and little else) about doubled (48.1 unfertilized vs. 92.4 mg m^{-2} dw fertilized), but this difference was only evident when the authors removed the 1988 pre-fertilization data from the comparison. Smolt sizes remained unchanged (1.46 g unfertilized vs. 1.48 g fertilized), but smolt densities doubled (207 ha^{-1} unfertilized vs. 433 ha^{-1}) and of course smolt biomasses increased (302 g ha^{-1} fertilized vs. 641g ha^{-1} unfertilized). In two of the fertilization years, increased smolt densities were due to increased spawner abundance, or increased spawners plus stocking, but during one year (1995) smolts per spawner increased from 25 to about 150 per female. This was not observed in the year previous or the year following 1995 and no explanation is offered. In summary, the data suggest that although Coghill Lake was relatively unproductive (meromictic and glacially influenced) and although smolt weights did not change, fertilization was associated with a doubling of smolt densities, and therefore a doubling of smolt biomass.

Chilko Lake - British Columbia: - Chilko Lake (18,500 ha) was fertilized for 5 years (1988, 1990-93) (average 5480 g N and 499 g P ha^{-1} y^{-1}) and comparisons were made with 6 unfertilized years (1984-86, 1989, 1994-95) (Bradford et al. 2000). During the fertilized years, there were significant increases in total phosphorus (TP fertilized mean 4.1 vs. unfertilized 2.7 µg L^{-1}) and primary production (1^{O} production fertilized mean 175 vs. unfertilized 102 mg C m^{-2} d^{-1}). Other limnological parameters were also greater during the fertilized years: (i.e. mean summer chlorophyll a 1.2 fertilized vs. 0.9 µg L^{-1} unfertilized; mean summer zooplankton biomass 1119 fertilized vs. 829 mg m^{-2} unfertilized), but variability was high and the differences were not significant. During the fertilized years, the size of age-1 smolts increased by 34% and the size of age-2 smolts increased by 58%. Recruits per spawner was also 73% higher during fertilized years, but the confidence interval was large (-2% to 174%). Finally, fertilization was associated with a weak (but positive) relationship between percent marine survival and smolt size.

Field studies with more complex results (Summarized in Table 1).

Great Central Lake- British Columbia 1969-76: As noted above, the concept of sockeye nursery lake fertilization grew out of a series of exceptionally forward-looking experiments started in 1969 at Great Central Lake (GCL). The early work reported by Parsons et al. (1972), LeBrasseur and Kennedy (1972), Barraclough and Robinson (1972) suggested that during the first year of fertilization, GCL produced an almost perfect donor-control response. Algal production and zooplankton biomass increased, and juvenile sockeye grew more quickly. These early reports were followed by others summarizing data collected during 1969-76 (LeBrasseur et al. 1978). During 1969-76, the lake was fertilized (average 5184 g N and 1227 g P ha^{-1} y^{-1}) for four years (1970-73) and not fertilized for four years (1969, 1974-76). Comparisons between the fertilized and unfertilized periods, revealed that fertilization was associated with a doubling of epilimnetic primary production (mean production 5 unfertilized vs. 11 g C m^{-2} y^{-1} fertilized), and a near doubling of chlorophyll a (mean concentrations 7 unfertilized vs. 11 mg m^{-2} fertilized). Mean growing season zooplankton biomass increased by a factor of approximately 8 (mean 0.9 unfertilized vs. 7.4 g m^{-2} fertilized). Acoustic estimates of juvenile numbers showed lower densities during the fertilization years (treatment mean counts of 2500 unfertilized vs. 1860 juveniles ha^{-1} fertilized). Comparisons of age-1 smolt sizes showed a slight increase during the fertilized years (mean annual weights 2.78 g unfertilized vs. 3.13 g fertilized) (mean fork length 68 mm unfertilized vs. 70 mm fertilized). Comparisons of age 2 smolt weights showed much larger differences (mean annual weight 4.3 g unfertilized vs. 9.93 g fertilized), but age 2 smolts comprised only an average of 3.5% of the population during the fertilized years and there was also some uncertainty about smolt aging, so that some of the age 2 smolts could have been age 3. During the fertilization years, percent egg to fall-fry survival almost doubled (mean 5.2% unfertilized vs. 10.3 % fertilized) and the authors note that marine survival also increased (numbers of returning adults ca. 58,000 y^{-1} from non-fertilized years vs. ca. 218,000 y^{-1} from fertilized years). However, given that the fertilized fry were only slightly larger than the unfertilized fry, it is difficult to explain this increase in marine survival (attributed to increased smolt weights). In addition, the authors note that during the 1970s, escapement into Sproat Lake (a lake adjacent to GCL that shares the Barkley Sound stock) also increased. This was confirmed by Hyatt and Steer (1987) who showed that commencing in 1973, the entire Barkley Sound stock increased about five fold, and that the pattern observed for the Sproat Lake stock almost exactly mimicked the pattern seen for GCL. It is difficult to attribute this to fertilization, since the

Sproat Lake stock was not fertilized. Hyatt and Steer (1987) conclude that "there are many unanswered questions concerning the role of lake fertilization in promoting the increased returns of sockeye to GCL and in the intervening years many alternate hypotheses have been suggested as explanations for the increase".

More about British Columbia LEP nursery lakes: The Lake Enrichment Program began in 1977, lasted for more than 10 years and involved various levels of fertilization of 17 sockeye nursery lakes. Summary reports (Stockner and Hyatt 1984, Shortreed et al. 2001) compared preliminary limnological results from several of these nursery lake fertilization studies. They also anecdotally noted that: (1) Kennedy-Clayoquot developed blue-green algal blooms which were corrected with increased N:P ratio fertilizers (i.e. more N). (2) Nimpkish Lake developed blooms of *Rhizosolenia*, a large diatom that acted as a nutrient sink. They predicted that this could be corrected by reducing N:P ratios. (3) Great Central Lake was prone to the development of hypolimnetic blue-green plates, and they predicted that this problem could be corrected by increasing N:P ratios. (4) A year after the onset of fertilization, Long Lake juvenile sockeye growth rates increased and smolt size doubled relative to untreated year performance. However, by year two of the fertilization, Long Lake had developed a very large stickleback population (>5000 ha^{-1}) and juvenile sockeye growth rates plummeted (McKinnell et al. 2001).

Additional LEP data pertaining to limnological responses to lake fertilization were reported in a series of papers published during the 1980s. Stockner and Shortreed (1985) analyzed 1980-83 phosphorus, nitrogen, chlorophyll and primary production data from 17 fertilized coastal nursery lakes and verified highly significant bottom-up relationships (Dillon and Rigler 1975) between phosphorus concentration and various measures of algal biomass and production. Stockner (1987) noted that coastal food chains (picoplankton → protozoans → microzooplankton → zooplankton → sockeye) tended to be longer and therefore perhaps less efficient than food chains found in more eutrophic interior British Columbia nursery lakes. Also focusing on lower trophic levels, Stockner and Shortreed (1988) provided a detailed analysis of water chemistry and algal data from Kennedy Lake. The Clayoquot Arm (CA) of Kennedy Lake was fertilized from 1978 to 1984. In 1981-82 a substantial fall bloom of *Anabaena circinalis* was observed. During 1978 the fertilizer molar N:P ratio was 10:1 and in 1979-81 it was 15:1. Since *A. circinalis* was known to be a nitrogen fixer, it was assumed that the blooms were due to a nitrogen shortage, so during 1982 the fertilizer molar N:P ratio was increased to 26:1 and during 1983-84 increased again to 35:1. The result was that during 1983-84, *Anabaena* disappeared almost entirely, but was replaced by large blooms of *Rhizosolenia* sp., a non-grazable diatom. This bloom disappeared in 1985 when fertilization was suspended. At Sproat Lake, Shortreed and Stockner (1990) reported that *Rhizosolenia eriensis* was the dominant species in the epilimnion during the spring but during the summer, was restricted to a deep chlorophyll maximum (DCM) at the bottom of the epilimnion (20-25 m) and consequently was not influenced by fertilization during 1985 when fertilizers were added slowly over 18 weeks. However, during 1986, when the entire fertilizer load was applied over 8 weeks, epilimnetic algal densities increased to such an extent that the light penetration into the upper hypolimnion was reduced and production at the DCM declined resulting in a net loss of algal biomass available to grazers. The authors concluded that at Sproat Lake, fertilization may have decreased rather than enhanced food availability for sockeye.

Sockeye data from selected LEP nursery lakes were summarized by Hyatt and Stockner (1985). Using 38 years of data from fertilized and unfertilized lakes, they found significant correlations between: age-1 smolt weight and mean summer zooplankton biomass ($r^2 = 0.22$, $n = 38$, $p< 0.003$) and an even better correlation between age-1 smolt weight and mean summer zooplankton biomass per juvenile sockeye ($r^2 = 0.44$, $n = 38$, $p< 0.001$). They also found a negative relationship between age-1 smolt weight and summer-fall juvenile density (r2 = 0.52, $n = 38$, $p <0.001$). Finally they found that smolt sizes in unfertilized lakes, were on average, smaller than in fertilized lakes having similar juvenile densities. Taken together these relationships all strongly suggest that in the LEP study, no matter what problems may have occurred with algae, lake fertilization was associated with the production of larger age-1 smolts. Although the authors gave several examples from lakes such as Owikeno and Babine, demonstrating a positive relationship between sockeye smolt size and increased marine survival, they did not provide similar data from any of the fertilized or unfertilized LEP lakes.

Hobiton Lake - British Columbia: Hardy et al. (1986), summarized the results of the Hobiton Lake fertilization experiment. Hobiton Lake (360 ha) is located on the west coast of Vancouver Island. It was fertilized (average 5840 g N and 861 g P $ha^{-1} y^{-1}$) during 1980-83 and not fertilized in 1984. Comparisons of data from the 4 fertilized years vs. the single unfertilized year show that fertilization was associated with higher phosphorus concentrations (mean annual concentration 3.2 fertilized vs. 2.1 μg L^{-1} unfertilized), higher chlorophyll a concentrations (mean annual concentration 2.2 fertilized vs. 1.3 μg L^{-1} unfertilized), but lower zooplankton densities (mean annual density 3700 fertilized vs. 4300 m^{-3} unfertilized), and little change in fish density (mean annual density 1623 fertilized vs. 1576 ha^{-1} unfertilized). Mean summer TN:TP was 50:1 during fertilization and increased to 129:1 after (during 1984). This was associated with a large post-fertilization (1984) bloom of *Rhizosolenia* sp.

Adams Lake - British Columbia: Adams Lake (12900 ha) located in south-central British Columbia, was fertilized for one year (5040 g N and 540 g P $ha^{-1} y^{-1}$) during 1997. Water chemistry (Hume et al. 2003) was reported for a control year (1986) and for the fertilized year (1997). Fertilization was associated with higher phosphorus concentrations (mean summer particulate P 1.2 unfertilized vs. 2.7 μg L^{-1} fertilized) less nitrate (mean summer NO_3 77.1 unfertilized vs. 61.6 μg L^{-1} fertilized), and more chlorophyll a (mean summer chlorophyll a 0.87 unfertilized vs. 0.97 μg L^{-1} fertilized). During the fertilized year, there was an increase in all of the major zooplankton species (*Daphnia thorata*, *Eubosmina longirostris*, *Diacyclops bicuspidatus thomasi*, and *Leptodiaptomus ashlandi* (mean summer biomass unfertilized 590 vs. 743 mg m^{-2} dw fertilized). During the fertilized years, sockeye diets comprised >80% *Daphnia* plus 10% other cladocerans. Copepods were seldom consumed. Comparisons of smolt weights from an unfertilized brood year (1992) with smolt weights from the fertilized brood year

(1996), suggested that fertilization was associated with increased growth rates (mean smolt weight unfertilized 2.64 g vs. 3.58 g fertilized).

Yakoun Lake - British Columbia: Yakoun Lake (810 ha) located on the Queen Charlotte Islands was fertilized (3563 g N and 533 g P ha^{-1} y^{-1}) during 1983-85. Water chemistry (Stockner and Shortreed 1985) was reported for a control year (1982) and for the first year of fertilization (1983). Sockeye data (Hyatt and Rankin 1996, Rankin and Hyatt 2002) were reported for many of the years between 1982 - 1998. Fertilization was associated with increased nutrients (mean summer TP 1.9 unfertilized vs. 4.0 μg L^{-1} fertilized), (mean summer TN 187 unfertilized vs. 288 μg L^{-1} fertilized) and increased chlorophyll a concentrations (mean summer chlorophyll a 1.69 unfertilized vs. 3.28 μg L^{-1} fertilized). The fish data were more complicated. The first complication was that brood-year escapement for the fertilized years was exceptionally high averaging 13,333 fertilized vs. only 7,838 adults for the unfertilized years. This meant that potential egg deposition was higher during the fertilized years (16.6 million fertilized vs. 9.9 million unfertilized). The second factor that complicated the interpretation of the sockeye data was that during 1982-86, Yakoun Lake had exceptionally large stickleback populations. During this period, stickleback densities averaged 1846 ha^{-1} while juvenile sockeye densities averaged only 922 ha^{-1}. Curiously after 1987, the stickleback all but disappeared from Yakoun Lake. The expected effect of both increased fry recruitment and high stickleback densities, was increased competition for food leading to potentially lower growth rates. In fact, plots of sockeye fall weights with respect to total fish density (sockeye fry plus stickleback) clearly showed that when densities were > 1800 total fish ha^{-1}, sockeye growth rates did decrease (Hyatt and Rankin 1996). Therefore, in an attempt to make meaningful comparisons for in-lake juvenile sockeye assessed during the fertilized years (1983-86) and the unfertilized years (1982, 1986-99) we restricted our unfertilized data set to include only those years when total fish densities >1500. For this selected unfertilized data set (including 1981, 1986-89, 1995), total fish density (sockeye + stickleback) during the fertilized years was 2775 ha^{-1} vs. 2214 ha^{-1} unfertilized. The density of sockeye alone during the fertilized years was 709 ha^{-1} vs. 1528 ha^{-1} unfertilized, and of course stickleback density during the fertilized years was 2066 ha^{-1} vs. 686 ha^{-1} unfertilized. Fertilized vs. unfertilized comparisons for sockeye, showed that fertilization was associated with: higher fall-fry weights (2.47 g fertilized vs. 1.12 g unfertilized), but lower sockeye production (1.7 fertilized vs. 2.7 kg ha^{-1} unfertilized). Note that during the fertilized years, total fish production (sockeye plus stickleback) was higher (4.2 fertilized vs. 3.7 kg ha^{-1} unfertilized), but during the fertilized years, egg-to-fall fry survival was much lower (6.7 % fertilized vs. 11.2 % unfertilized). Although fertilization was associated with increased overall total fish production and also with larger sockeye fall-fry, the differences were not statistically significant (t test $p = 0.41$) and (t test $p = 0.08$). Also during the fertilized years, sockeye densities and sockeye production was lower than during the unfertilized years.

Muriel Lake: At Muriel Lake (Hyatt et al. in review), the objective was to investigate the potential competitive interactions between juvenile sockeye, threespine stickleback (*Gasterosteus aculeatus*), and the shrimp *Neomysis mercedis*. The lake was fertilized with slow release pellets during 1984. A series of smolt samples were taken during 1982-89, and suggested that age 1 and age 2 smolt weights and lengths did not increase during the fertilization period. Also, during 1985-86 bioenergetic assessments were used to measure biomass, production and consumption for sockeye, stickleback and *Neomysis*. This analysis suggested that *N. mercedis* could consume 7-8 % of the zooplankton standing stock per day, while 0+ and 1+ sockeye consumed only 0.8 % d^{-1}. Threespine stickleback consumed < 0.2 % d^{-1}. Although *N. mercedis* was the main consumer of zooplankton, they were themselves consumed by fish. During the summer of 1986, an increase in the relative numbers of 1+ sockeye was associated with substantial declines in *Neomysis* biomass. Although this came too late in the season to benefit 1986 Muriel Lake sockeye, it did serve to highlight the importance of pelagic food web trophic triangles in controlling food supplies to sockeye. The authors suggested that during years when exogenous recruitment events result in high sockeye fry recruitment, *Neomysis* populations could be held in check by 0+ and especially 1+ sockeye. During years when sockeye fry recruitment and biomasses were low, zooplankton consumption rates by *Neomysis* would be so high, that sockeye could gain little benefit from fertilizer-induced enhancement of the zooplankton food base. The authors concluded that *Neomysis* lakes should only be fertilized when sockeye densities are relatively high.

Pass Lake and Esther Pass Lake - Alaska: The objective of the Pass and Ester Pass experiment (Koenings and Kyle 1997) was to test the hypothesis that overgrazing by strong sockeye year classes could restructure the zooplankton assemblages of fertilized lakes to such an extent that they were slow or even unable to respond to lake fertilization. Their results clearly demonstrate the effects of overstocking.

The Ester Pass (0.2 km^2) experiment lasted 4 years and included: one un-stocked control year (1985), two years (1988-89) of stocking (approximately 600,000 fry per year), and one year (1990) when stocking was discontinued. The lake was never fertilized. During the stocking years, mean smolt weights remained about constant (means of 5.4 and 4.8 g) and mean smolt biomasses remained about constant (68 and 72 kg). During the stocked years, mean summer zooplankton biomasses declined from 402 mg m^{-2} (control year 1985), to approximately 65 mg m^{-2}. When stocking was halted (1990), zooplankton biomass rebounded to 184 mg m^{-2} The authors concluded that Esther Pass Lake was not stocked beyond the EV model target level, and the post-stocking zooplankton community was able to retain its normal species composition, and size frequency characteristics.

The Pass Lake (0.5 km^2) experiment also lasted four years and included: an un-stocked control year (1985), two years (1988-89) of stocking (approximately 154,000 fry per year), and one year (1990) when stocking was discontinued. In addition, during the final two years (one stocked, the other not stocked), fertilizer was added. During the stocked years, mean smolt weights were low (means of 2.2 and 2.1 g), mean smolt biomass declined (158 to 45 kg), and mean summer zooplankton biomasses declined (783 mg m^{-2} during the control year 1985 to 13 mg m^{-2} during 1989). When stocking was halted and fertilizers applied (1990), zooplankton biomass remained depressed at 10 mg m^{-2} The authors state that Pass Lake was obviously overstocked, and that the zooplankton community was unable to retain its normal species composition and size frequency characteristics. The severe degradation of the Pass Lake zooplankton community may have been due to the fact that Pass Lake TP was lower than Esther Pass Lake (2.6 vs. 3.2 µg L^{-1}) and more importantly, during the first year of stocking, Pass Lake fry survival was high (12%) and smolt biomass was almost 3 times higher than at Esther Pass Lake. The effect was the almost complete elimination of all cladocerans from Pass Lake, and thus the elimination of the reproductive potential during subsequent years. The authors concluded that the bottom-up effects of fertilization were unable to counter-balance the top-down, density-dependent effects of overstocking.

Packers Lake - Alaska: Kyle (1994) analyzed the first 12 years of the data set for Packers Lake (2.1 km^{-2} located on Kalgin Island, Cook Inlet, Alaska) and Mazumder and Edmundson (2002) reanalyzed those data and added an additional four years. In an attempt to concisely summarize this complex 16 year data set, we have divided the chronology into four sections: (1) During years 1 and 2 (1981-82), base-line data were collected and there was no stocking and no fertilization. (2) During years 3-6 (1983-86) the lake was fertilized but not stocked. (3) During years 7-12 (1987-92), the lake was both fertilized and stocked. (4) During years 13-16 the lake was also fertilized and stocked, but N loading and stocking rates were reduced. Comparisons of time periods 1 & 2: (unfertilized vs. fertilized-not stocked) yield the following results: During period 2, (1983-86) fertilization rates were very high (17400 g N and 1760 g P ha^{-1} y^{-1}) and this was reflected in: higher TP concentrations (mean summer 14.7 unfertilized vs. 15.0 µg L^{-1} fertilized), higher chlorophyll a concentrations (mean summer 1.3 unfertilized vs. 2.0 µg L^{-1} fertilized) and higher zooplankton biomasses (mean summer 200 unfertilized vs. 349 mg m^{-2} dw fertilized). This was associated with large increases in smolt weights (age 1 - 5.2 g unfertilized vs. 10.4 g fertilized) and total smolt biomass increased by 65 % (mean annual 2000 kg unfertilized vs. 3300 kg per Lake fertilized). Smolt age composition changed from 8 % age 1 unfertilized to 42 % age 1 fertilized. Marine survival also increased (survival from smolt - returning adults 9.5% unfertilized vs. 13.6 fertilized). Comparisons of time periods 1 & 3: (unfertilized vs. fertilized & stocked) yield the following results: During period 3, (1987-92) fertilization rates were reduced (619 mg P ha^{-1} y^{-1}) and this was reflected in the following control-treatment comparisons: TP concentrations declined (mean summer 14.7 unfertilized vs. 15.0 period 2, vs. 13.0 µg L^{-1} period 3), chlorophyll a concentrations remained unchanged (mean summer 1.3 unfertilized vs. 2.0 period 2, vs. 2.0 µg L^{-1} period 3), zooplankton biomasses declined (mean summer 200 unfertilized vs. 349 period 2, vs. 200 mg m^{-2} dw period 3). This was associated with large declines in smolt weights (age 1 - 5.2 g unfertilized vs. 10.4 period 2, vs. 3.4 g period 3). Smolt age composition greatly favored age-1 smolts early in period 3, but declined back to near pre-fertilization levels by the end of the period. During period 2 fry stocking rates averaged 3,000,000 fry y^{-1} (>14,000 h^{-1}), however because mean smolt sized decreased, overall smolt biomass also decreased (mean annual 2000 kg period 1 - unfertilized vs 3076 kg period 2 - fertilized vs. 2700 kg period 3 - stocked and fertilized). Marine survival data were unavailable. Comparisons of time periods 1 & 4: (unfertilized vs. fertilized & stocked) yield the following results: During period 4, (1993-96) fertilization rates were further reduced (480 mg P ha^{-1} y^{-1}). TP concentrations declined (mean summer 14.7 unfertilized vs. 9.0 µg L^{-1} period 4), chlorophyll a concentrations remained stable (mean summer 1.3 unfertilized vs. 2.0 µg L^{-1} period 4), zooplankton biomasses continued to decline (mean summer 200 unfertilized vs. 149 mg m^{-2} dw period 4). Smolt weights and biomass remained about as they were in period 3. Marine survival data were unavailable.

In summary, period 2 fertilization (no stocking) was associated with much larger smolt weights and a 65% increase in smolt biomass. Period 3 and 4 treatments (fertilization and stocking) resulted in much smaller smolts and a reduction in total smolt biomass. At Packers Lake, fertilization alone produced much better overall results and better rates of smolt production than fertilization plus stocking.

Redoubt Lake - Alaska: Kyle et al. (1997) summarized a portion of the Redoubt Lake (1280 ha) data set for 1980-83 (unfertilized) and 1984-86 (fertilized with 15600 g N and 1530 g P ha^{-1} y^{-1}). Fertilization was associated with increased concentrations of chlorophyll a (0.76 unfertilized vs. 1.20 µg L^{-1} fertilized), higher zooplankton biomasses (100 mg m^{-2} unfertilized vs. 150 mg m^{-2} fertilized) and higher 2 year old smolt weights (4 g unfertilized vs. 10 g fertilized).

Snake River Sockeye: Declining returns of sockeye to the Snake and Salmon Rivers (headwaters of the Columbia) have been largely attributed to the construction of 8 dams in the Columbia corridor. Only 16 spawners returned between 1989 and 1994. In 1991, Snake River sockeye were listed under the U.S. Endangered Species Act, as being endangered. This prompted several preliminary studies followed by 4 years of fertilization at Redfish Lake.

Gross et al. (1998) constructed a nutrient loading model for the lake, and then predicted the likely long-term consequences of lake fertilization. The model suggested that under pre-dam conditions the annual return to Redfish Lake would have been 3,800 sockeye and that this would have contributed about 3% of the annual nutrient load received by the lake. The model also suggested that 3 years of lake fertilization would stimulate sockeye production, but that the effects would almost disappear after 8 post-fertilization years. They concluded that permanent effects could only be achieved by increasing smolt-to-adult survival rates.

Budy et al. (1998), reported results from Redfish Lake enclosures (350 m^3) treated with fish (juvenile kokanee) and nutrients (added to the metalimnion). The objectives were to assess the potential impacts of fertilization on water clarity (Redfish is a highly valued recreation area) and to assess the potential to increase juvenile sockeye growth rates. They found that: fertilization substantially increased chlorophyll (150%), primary production (250%), zooplankton biomass (200%) and that water clarity was reduced by 2- 4 m (Secchi disk). However, fish growth increased very little (15%) and even then it was likely that increased growth rates were due to the fact that the enclosures were fertilized (and zooplankton biomasses increased) for several weeks before fish were added. The authors concluded that fertilization in conjunction with removals of resident kokanee could benefit anadromous sockeye.

Luecke et al (1996) used a food web model to assess various management strategies for stimulating sockeye production in Redfish Lake, and concluded that fertilization in conjunction with removals of kokanee could benefit anadromous sockeye. They knew from earlier cage studies that kokanee densities in Redfish Lake were near carrying capacity and the model suggested that if the kokanee were left unchecked, >98% of fertilizer-enhanced *nerka* production would accrue to kokanee. They recommended that given a fertilization rate of 715 kg P y^{-1} (per lake), a reduction of 50-70% of the 0+ kokanee would be required in order to ensure that increased fertilizer-induced zooplankton biomass would benefit stocked anadromous sockeye fry.

Based on the above preliminary studies, Redfish Lake (615 ha) was fertilized during 1995-98 (Griswold et al. 2002). The data comprised three pre-fertilization years (1992-94) and four fertilized years (1995-98) and included both an experimental lake (Redfish) and an unfertilized control lake (Stanley). The *nerka* populations in both lakes comprised a mix of kokanee and stocked anadromous juvenile sockeye. At Redfish Lake, fertilizer was added at an average rate of 281g P and 5265 g N ha^{-1} y^{-1}. Comparisons of pre- and post fertilization years showed that during the fertilization: Secchi depth declined, chlorophyll a increased (0.5 pre-fertilization to 1.0 μg L^{-1} fertilized), zooplankton biomass increased (7.9 pre-fertilization to 10.3 μg L^{-1} fertilized), *Daphnia* biomass increased (0.8 pre-fertilization to 2.6 μg L^{-1} fertilized) and fish density increased (240 ha^{-1} pre-fertilization to 301 ha^{-1} fertilized) primarily due to sockeye stocking. Also the authors noted that post-manipulation *nerka* survival improved from 6.7 % to 19.7 %, but they also state that these changes could have been due to changes at the hatchery which produced higher quality fish during the fertilization period. Changes in juvenile lengths and weights were not assessed. Stanley Lake was monitored as a control, and during the pre- and post-manipulation time periods, Stanley Lake chlorophyll increased slightly, *Daphnia* biomasses declined slightly, total zooplankton biomass did not change and fish density (kokanee plus a few stocked sockeye) increased from about 100 to 400 *nerka* ha^{-1}. Changes in juvenile lengths and weights were not assessed. The authors note that climatic changes coincided with the pre- and post-fertilization periods and confounded experimental outcomes. They also noted that it was possible that the kokanee in Redfish Lake may have disproportionately benefited from lake fertilization (see Luecke et al. 1996 above) and that the planned 1999 fertilization was suspended for that reason. Also, due to concerns for esthetic values (clear water) the amount of fertilizer added (200 kg P y^{-1}) was less than recommended (see Luecke et al. 1996) and this may have weakened the anticipated bottom-up response by sockeye salmon.

Summary of general outcomes

Assumption 1: At the outset we noted that the potential success of sockeye nursery lake fertilization is predicated on the assumption that donor-controlled trophic transfers between nutrients → algae → zooplankton → fish; are both predictable and strong enough to yield increased smolt survival and size. Overall the preceding literature suggests that this is true and that lake fertilization is associated with increased biomasses (and/or production) of phytoplankton, zooplankton and juvenile sockeye (Table 1). At the bottom of the food web 11/13 between-year, treatment-control studies, showed that when fertilizers were applied, epilimnetic TP increased. For chlorophyll a, 22/22 studies showed positive responses to fertilization. This was especially clear for the two most heavily loaded lakes (Leisure 3455 g P ha^{-1} y^{-1} and Bonilla 2696 g P ha^{-1} y^{-1}). For zooplankton, responses to fertilization were generally more muted, but the trend was still very clear. 16/17 studies showed an increase in zooplankton biomass following fertilization. Two studies showed exceptionally large increases in zooplankton biomass. In the case of Leisure Lake, the loading rates were very high (3455 g P ha^{-1} y^{-1}), but in the case of Great Central Lake (LeBrasseur et al. 1978) the loading rates were quite ordinary and the very large increases in zooplankton biomasses may have been due to the fact that they were associated with sockeye densities and biomasses that were lower (due to poor escapement) during the fertilized years than during the unfertilized years. Responses from sockeye also suggested that fertilization was associated with increased growth and survival. 16/18 studies showed increased smolt (or fall-fry) weights during fertilization treatment years. Again the two exceptions were from Packer Lake comparisons 2 and 3 when probable overstocking and under-fertilization compromised the outcomes. It should be noted that for Packer Lake, comparison 1 (unfertilized vs. fertilized but not stocked), smolt weights increased by 100%. At Leisure Lake (most heavily fertilized), gains in smolt weights exceeded 100%, but for Bonilla Lake (second highest rate of fertilization) the gain was more modest (+ 39%). In 12/14 experiments, fertilization was associated with increased smolt production. Leisure Lake was again a standout showing an increase of > 250%. GCL recorded a loss due to poor escapement and little increase in smolt weight and Yakoun recorded a loss due to competition from sticklebacks. Finally, egg-to-fry survival rates were recorded for four studies. At Leisure Lake, survival increased by 69%. At Coghill Lake, during one year (1995), smolts per spawner increased from 25 to about 150 per female, during the other two years there was no increase. At Chilko Lake, recruits per female increased by 73% and GCL egg-to-fall fry survival increased by almost 100%. On balance, although data are sparse, it seems likely that fertilization is associated with increased egg-to-fry survival, so that recorded increases in smolt biomass are likely due to increased survival and/or increased weight gains.

Assumption 2: We now turn our attention to the second assumption (larger smolts survive better at sea). As noted, Ricker (1962) showed that over a broad geographical range, there is a positive relationship between sockeye smolt length and marine survival. This pattern has also been observed in between-year data from Owikeno and Babine Lakes (Hyatt and Stockner 1985), from the Karluk River (Barnaby 1944) and from Cultus Lake (Foerster 1954. The question is, do the weight gains that result from fertilization confer survival advantages in the marine environment. The data set is sparse, but in every case the answer is yes. At Leisure Lake, smolt weights increased by 112% and smolt-to-returning adult survival increased by 25%. At Packers Lake (comparison 1 - Kyle 1994) smolt weights increased by 100% and marine survival increased by 43%. At Chilko Lake, each one gram increase in smolt weight was associated with a 14% increase in the rate of adult returns. It should be noted that these results depend on rather small numbers of lake-years, and that variability in the data is large and statistical significance is weak. On the other hand, there are no studies that show reduced marine survival. From this we suggest that it seems likely that lake fertilization is associated with increased marine survival of sockeye salmon. Clearly more data are needed to fully verify this conclusion.

Summary of some lake-fertilization food web problems and their solutions

Although virtually all of the studies summarized above suggest that lake fertilization is likely to yield positive gains in smolt biomass and may even contribute to increased marine survival, they also suggest that problems are possible - even likely. This is not surprising. Freshwater food webs are relatively complex, and when entire lakes are fertilized to enhance the production and survival of anadromous sockeye, it is almost certain that unexpected results will emerge. Based on the preceding literature review, six potential "problems" have been identified. The first deals with some of the myths and realities of phosphorus loading. The other five with technical problems, some resolved, others not.

(1) The very first lake fertilization at Great Central Lake (1969) was prompted by the suggestion that declines in sockeye might be partially explained by the "smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners" (Foerster 1968). Recently, stable isotope studies (reviewed in Cederholm et al. 1999) have shown that marine-derived N and C is found in lake, stream and terrestrial biota and that watersheds with higher escapements have more marine derived N in some terrestrial species (Reimchen et al. 2003). These data, combined with escapement and mass-balance analyses, leave little doubt that sockeye salmon carcasses contribute to the nutrient regimes of sockeye rivers and streams (reviewed in Naiman et al. 2002). For sockeye nursery lakes, there is also evidence which suggests that carcasses can make significant contributions to nutrient budgets, but conclusions seem to be very lake-dependent. The evidence that is generally cited (Kyle et al. 1997, Naiman et al. 2002) to support the case for the importance of carcasses is primarily based on two lakes. The first is Lake Dalneye, Kamchatka, Russia, where Krokhin (1967) used a 24 year (1937-60) data set to estimate phosphorus inputs and losses and concluded that low sockeye returns during 1948-60 were associated with negative phosphorus balances (inputs - losses) to the lake. The second is Karluk Lake, Kodiak Island, Alaska, where Juday et al. (1932) was the first to suggest that primary and secondary production was strongly influenced by sockeye salmon carcasses. Also, Nelson and Edmondson (1955), overviewed Karluk Lake data up to 1953, and then went on to clearly outline the fertilizer enhancement theory (carcasses → nutrients → phytoplankton → zooplankton → increased food consumption by fry → larger smolts → increased marine survival) that is accepted today. Finally, Schmidt et al (1998) provided a sophisticated review and analysis of Karluk Lake sockeye data and concluded that carcasses could account for 40 % or more, of the phosphorus in Karluk Lake. They also suggested that there was a clear relationship (although confounded by fertilizer additions during the mid-1980s) between lake July-August TP concentrations

and fertilizer derived from carcasses deposited during the pervious year. Ricker (1937) acknowledged the Karluk Lake data (Juday et al. 1932), but stated that at Cultus Lake "even the largest runs would not be sufficient to add greatly, on decomposition, to the dissolved supply [of nutrients] already available". He pointed out that this was due to the fact that run density (per cubic meter of lake water) was 10 times higher in Karluk Lake than in Cultus Lake, and that Cultus Lake turnovers are high resulting in the loss of at least ½ of the nutrient load each year. Also, Gross et al. (1998) used the Redfish Lake simulation model (see above) to estimate that carcasses accounted for only about 3% of the annual historical total nutrient load to the lake, even before the advent of hydroelectric dams. Finally, at Coghill Lake, Edmundson et al. (1997) estimated that carcasses contributed 10% of the annual load. From all of this it may be wise to conclude that the contribution of carcasses varies considerably from lake-to-lake. Factors such as spawner numbers, redd locations, lake volumes, watershed areas, turnover times and the timing of flushing events; all influence historical and current contributions made by carcasses.

Several lake fertilization problems are associated with nutrients and algae. (2) In Great Central Lake, Stockner and Hyatt (1984) reported the development of hypolimnetic blue-green plates and they suggested that this problem could be corrected by increasing N:P ratios. (3) Also Stockner and Hyatt (1984) and Stockner and Shortreed (1988) reported that when low N:P fertilizer ratios (low N) were added to Kennedy-Clayoquot, an *Anabaena* bloom developed. When the fertilizer having a higher N:P ratio (increased N) was applied, the blue green bloom disappeared. (4) Finally, Stockner and Hyatt (1984) and Stockner and Shortreed (1988) reported that when higher N:P ratio fertilizer was added to Kennedy-Clayoquot, a *Rhizosolenia* bloom developed. Stockner and Hyatt (1984) also reported that during 1982 when 15:1 fertilizer was added to Nimpkish Lake, *Rhizosolenia* bloomed, but when the ratio was reduced to 1:1 (unpublished data), *Rhizosolenia* became far less abundant. *Rhizosolenia eriensis* also appeared at Woss Lake during both 2000 and 2003. *R. eriensis* cells resemble large "glass-like" cylinders, measuring approximately 75 x 6 x 4 µm and having spines at each end . This shape ensures that they are non-grazable and it also allows individual cells to absorb considerable quantities of nutrients that might otherwise fuel the growth of grazable species. Over the four year fertilization period at Woss Lake, only 20% of the available algae were grazable, and during *R. eriensis* blooms, percent grazable algae fell to 2 - 5% by volume. *Rhizosolenia* was also reported at Mohun Lake (Perrin et al. 1986) where densities increased when fertilizer was added. Also at Hobiton Lake which was fertilized during with a 1980-83 (Hardy et al. 1986). During fertilization, the epilimnetic N:P ratio was 50:1. When fertilization stopped in 1984, mean summer N:P increased to 129:1 and this was associated with a large bloom of *Rhizosolenia* sp. Finally, Hardy et al. (1986) report that (MacIsaac pers. comm.) found that in the laboratory, *Rhizosolenia* grew better with a high N:P ratio. It appears that the potential key to *Rhizosolenia* control is to reduce the N:P ratio in the fertilizer. The obvious problem is that too little N is widely associated with the growth of blue-green algae, but this too may be partially controlled by the fact that blue greens like *Anabaena*, are most common in lakes with warm, shallow, stable epilimnia and are seldom found in windy coastal lakes like Henderson Lake, Chilco Lake and Woss Lake, even when N:P ratios are low (less nitrogen). Clearly, before additional coastal-lake fertilizations are attempted, lake-specific information pertaining to algal species composition and preferences for physical-chemical conditions is highly recommended.

The final two lake fertilization "problems" deal with fish and zooplankton. (5) Hyatt and Stockner (1985) reported that after the onset of fertilization, Long Lake developed a very large stickleback population and juvenile sockeye growth rates did not respond positively to fertilization (McKinnell et al. 2001). O'Neil (1986) and O'Neill and Hyatt (1987), used enclosure manipulations to compare food preferences and consumption rates of threespine sticklebacks and juvenile sockeye. They found that both ate roughly the same food types and that consumption rates were about equal. As noted in the preceding case-study review, stickleback also caused competitive problems at Yakoun Lake. During the fertilization years, stickleback accounted for more than ½ of the fish in the lake, and the result was reduced sockeye yields. To date, there is no clear understanding of the factors that cause stickleback "outbreaks". Their appearance tends to be sporadic lasting a few years, after which they almost disappear, sometimes for 10-20 years at a time. (6) Finally, Cooper (1988), Cooper et. al. (1992), Ashley et al. (1999), and Hyatt et al. (in review), have all commented on the problems associated with competition between *Mysis* and juvenile sockeye. Concern is based on the fact that in Kennedy and Muriel Lakes, the mysid population could consume 5-10 times as much zooplankton as the juvenile sockeye population. No solutions have been offered, but Hyatt et al. (in review) note that sockeye (especially 1+ juveniles) consume substantial quantities of *Neomysis*, and they recommend that *Neomysis* lakes should only be fertilized when sockeye densities are high.

Overall, it seems likely that in general, the problems associated algae (blue-greens or large diatoms) are manageable. This is partially because alterations of N:P ratios have been shown to be effective (for blue-green algae at least), and also because even when algal problems have been encountered, increased zooplankton biomasses have still been associated with coastal lake fertilization (Hyatt and Stockner 1985). Briefly stated, it seems likely that when fertilizers are added to lakes, increased zooplankton biomass and production is almost guaranteed. More serious problems have occurred at the zooplankton → sockeye link in the food web. Aside from the obvious difficulties associated with competition from *Mysis* and sticklebacks, one must ask why the literature shows so much variation in fertilizer-induced increases in smolt sizes. It is very likely that these differences are due to between-lake differences in rates of energy flow from zooplankton to juvenile sockeye, but the problem is that these rates have not be measured for any of the nursery lake fertilizations described above. The solution is to estimate production rates for zooplankton taxa and then to compare these with bioenergetically-based consumption rates for juvenile sockeye. That is the primary objective of our study at Woss and Vernon Lakes.

Nimpkish sockeye history

Nimpkish sockeye have historically been of great importance to both the 'Namgis First Nation and the commercial fishery. In 1958, the Department of Fisheries (Canada) wrote that the Nimpkish fishery was "second in value only to that of the Fraser in the southern half of the Province" (DF - Canada: Anon 1958). Commencing in 1949, fisheries inspectors from the Canada Department of Fisheries began to survey adult salmon escapement into the Nimpkish Watershed. DF-Can continued these surveys every year from 1949-57. After that date the surveys were conducted by a variety of government agencies, contractors and, most recently, by personnel from the Gwa'ni Hatchery. These efforts have resulted in a long-term data set (Fig. 1 taken from NRMB 2002) that shows a continuous decline in sockeye escapement. It should be noted however, that the methods for escapement estimates have obviously been different over the years. In the 1950-1960 period sockeye abundance was determined by visual estimates in the main holding areas (e.g. Karmutzen pool at Woss) and numbers were probably underestimated. An exception during that period would be the year 1957, when a more thorough count was conducted as part of a Biological Survey of the Nimpkish River System to determine the potential for hydroelectric development on the Nimpkish. More intensive counting took place during the 1960-1980 period when DFO guardians conducted extensive walk surveys; however, no attempt was made to enumerate the Woss Lake spawning population. The 1980-1990 period saw increased enumeration effort by the Nimpkish Enhancement & Restoration Program; various tagging programs, dead pitches, fence counts, and aerial surveys resulted in more accurate estimates (ALBY 2000). The 'Namgis First Nation (Gwa'ni Hatchery) crews began regular swim surveys in 1995 and the relative reliability of sockeye abundance estimates has been regarded as high since that time.

There is little doubt that the changes in sampling methodologies described above are responsible for some of the variability seen in escapement data (Fig. 1). There are also questions about the causes of the decline. On one hand, the cause may well have been commercial over-fishing and habitat destruction by the logging industry. On the other hand, the greatest reduction in average returns appears to coincide with the 1975-77 temperature shift that has been well documented for North-Pacific waters (Peterman et al. 1998). Whatever the reason, the trend (Fig. 1) is strong and suggests that during the last 50 years, escapement and implicitly total returns, has declined by at least 90%. It was this trend that motivated the lake fertilization study described below.

Objectives and research protocol

The overall objective of the analysis that follows is to determine whether whole-lake fertilization of Woss Lake (Vancouver Island), could reliably increase the growth, production and survival of age-0 and age-1 juvenile sockeye salmon. Our approach was to gather four years of data at Woss Lake and to compare these with four years of data collected at an unfertilized reference lake (Vernon Lake). Because our protocol lacked extensive pre-fertilization data from Woss Lake, we adopted a detailed comparative analysis of food web dynamics in a treated and untreated lake to make inferences about the value of lake fertilization as a stock restoration technique. Specifically we quantified the biomass dynamics of all major phytoplankton taxa, calculated production and consumption for all of the major zooplankton species, calculated growth and production (bioenergetics model) for age-0 and age-1 sockeye and then calculated the species-specific consumption rates of sockeye on each of the major zooplankton taxa. Then throughout each growing season, we determined the proportion of mean annual species-specific zooplankton production and standing stock consumed by sockeye.

The protocol was as follows: (1) Beginning at the top of the food web, we measured sockeye growth rates, diets, diel migration patterns and water temperatures. These data were then used in a bioenergetic analysis to estimate species-specific food consumption by juvenile sockeye. (2) Throughout the sampling periods, we assessed species-specific zooplankton biomasses, lengths, weights, and egg numbers. (3) We then calculated the percentage of species-specific zooplankton production that was consumed by sockeye. In cases where sockeye consumption was greater than taxa-specific zooplankton production, we expected to see biomass declines in that taxonomic group. In cases where overall sockeye consumption was greater than the production of zooplankton target groups (determined from stomach analysis) we expected to see reduced sockeye growth rates. In cases where production by zooplankton target groups exceeded sockeye consumption we expected to see increased zooplankton biomass and increased sockeye growth rates. (4) Finally, because donor-control sockeye enhancement theory is based on the assumption that fertilizer additions stimulate algae that can be grazed by zooplankton, we monitored rates of nutrient addition and we completed species-specific assessments of algal species composition. Our objective was to determine whether the algal genera that were stimulated by the fertilizer additions were also grazable by zooplankton.

METHODS

SITE DESCRIPTION

Woss and Vernon Lakes (Figs. 2, 3) lie within the Nimpkish watershed, the largest on Vancouver Island (2,226 km^2) draining north into Broughton Strait directly across from Cormorant Island (Alert Bay). Detailed descriptions pertaining to the watershed are found in Muller (1975, 1977), Howes (1981), Matthews (1986) and are summarized in ALBY (2000) and NRMB (2002). The Nimpkish Watershed includes six known sockeye nursery Lakes. Four have been monitored periodically since 1978 (Table 2). Nimpkish Lake (surface area 36.5 km^2) is the largest (Rutherford et al. 1986) and on average, has contributed 46 % of the sockeye fry output from the watershed. Woss Lake is the second largest (surface area 13.3 km^2, Z_{max} 150 m), has a watershed (246 km ^{2}) which accounts for 11% of the total Nimpkish watershed area and on average has contributed 35 % of the sockeye fry output from the watershed. Vernon Lake is the third largest in the Nimpkish Watershed (surface area 8.4 km^2, Z max 102 m), lies in the Vernon Lake (Sebalhall) watershed (306 km ^{2}) which accounts for 14% of the total Nimpkish drainage area, and historically has averaged 16 % of the sockeye fry output from the watershed. The other three lakes (Schoen, Anutz and Klaklakama) are known to have been sockeye nursery lakes during the first ⅔ of the twentieth century, but now spawning sockeye are rarely observed.

Sampling and sample analysis

Sampling schedule: Woss and Vernon Lakes were sampled during 2000 - 2003 (Table 3). During the first three years, samples were taken approximately every 3 weeks. During the last year, sample frequency decreased.

Water Chemistry: Oxygen and temperature were measured at two stations on each lake, at 1 m depth intervals from 1-23 m using either YSI oxygen-temperature meter or a Hydrolab DataSonde. Chemical variables were measured every three weeks at 2 stations on each lake (Woss and Vernon). Variables included: epilimnetic and hypolimnetc TP, $NO_3 + NO_2$; and epilimnetic particulate P, C, N, and chlorophyll a. Epilimnetic samples were taken by combining three discrete samples collected at 1,3,5 m. Hypolimnetic samples were taken at 20 m. Samples for TP, $NO_3 + NO_2$ were filtered through 80μm nitex. Samples for particulate P, C, N, and chlorophyll a were unfiltered. TP samples, were placed in screw-cap test-tubes, returned to the laboratory and stored in the dark at room temperature. $NO_3 + NO_2$ samples were passed through an acrodisk filter, placed in screw-cap plastic bottles, returned to the laboratory and frozen. Unfiltered water for particulate P, C, N, and chlorophyll a samples was returned to the laboratory for filtration. Field-laboratory preparation for chlorophyll a, included volumetric filtering through a 47 mm millipore filter at 10 PSI, folding the filter and freezing in a 50 mm plastic petri dish wrapped in tinfoil. Particulate P was filtered through a 47 mm Whatman filter, folded and frozen in a screw-cap vial. Particulate C/N was filtered through a 25 mm GFF filter, folded and frozen in a 25 mm petri dish. Sample analysis was performed at the Cultus Lake laboratory, Department of Fisheries and Oceans.

Phytoplankton and zooplankton field & laboratory preparation: Phytoplankton samples were collected at 1, 3, 5 m, at each of two stations on each lake. Whole water was placed in 500 mL plastic jars and preserved with Lugol's solution. At the laboratory, the well-mixed samples were concentrated by sedimentation in graduated cylinders over a 5-day period. The concentrated samples were stored in evaporation-proof 28 mL screw-capped vials. Samples were diluted depending on the phytoplankton density and taxa were identified and enumerated using inverted microscopy at 300 and 600x magnifications. Utermöhl-type counting chambers of 2, 5 or 10 mL capacity were employed (Utermöhl 1958). Taxonomic (genus level) determination followed Bourrelly (1966, 1968, 1970). The taxonomy followed was:

- Division Chlorophyta
  - Class Chlorophyceae
  - Class Charophyceae

Division Chrysophyta
    Class Xanthophyceae
    Class Bacillariophyceae
    Class Chrysophyceae
    Class Prymnesiophyceae
    Class Synuraceae
Division Pyrrhophyta
    Class Dinophyceae
    Class Cryptophyceae
Division Euglenophyta
    Class Euglenophyceae
Division Cyanophyta
    Class Cyanophyceae
Division Rhodophyta
    Class Rhodophyceae

Completed counts totalled at least 300 units (cells, filaments or colonies) and 45 or more units of the taxa contributing most to the total biovolume were recorded. Counts were recorded as numbers of individual cells per genus. Also, individual cells were measured and their biovolume determined using formulae for basic geometric shapes (Vollenweider 1969, Rott 1981, Hopkins and Standke 1992). Biovolumes were recorded as cubic microns per mL divided by 1000. This equals mm^3 m^{-3}, and assuming that 1 mm^3 = 1 mg, this equals 1 mg m^{-3} or 1 µg L^{-1}. When colonial forms were counted, biovolume was determined by the measurement of the cells, not including the intercellular spaces that exist in certain genera. One of the objectives of the phytoplankton counting procedure was to assess the relative availabilities of edible (grazable) and non-edible (non-grazable) algae. We therefore attempted a qualitative assessment of "edibility" based on size, toxicity and digestibility. (1) Size: single cells or colonies < 30 *µ*m width or length were considered edible unless they were classified as being either "toxic" or "digestion-resistant" (defined below). These dimensions are in agreement with previously published thresholds (Cyr 1998; Cottingham 1999). (2) Toxicity: *Microcystis* was always classified as being "toxic". Other genera were assumed to be non-toxic. (3) Digestibility: algae with thick gelatinous sheaths can pass through *Daphnia* guts undigested (Stutzman 1995) and were considered to be digestion-resistant, independent of size. Abundances of digestion resistant algae were low.

Zooplankton samples were collected every 3 weeks, at each of 4 stations on Woss Lake, and 3 stations at Vernon Lake. Samples were collected using a metered (Rigosha and Co., Ltd. Model 5571) vertical haul net (square mouth 30 x 30 cm) (Filion 1991) winched at 1 m s^{-1} between 25-0 m. Two mesh sizes (100 µm and 250 µm) were used. Samples were placed in individual sample jars, preserved in 4% buffered and sugared formalin and returned to the laboratory. For each sample, the Rigosha counts were used to calculate net filtration efficiency. Then each sample was made up with preservative so that each one mL of sample contained water from 10 L of lake water. For each station, 10 mL (containing plankton from 100 L of lake water) from each sample jar was added to a "combined" sample jar. Since there were 4 stations at Woss Lake, the combined sample jar contained 40 mL of sample representing the zooplankton found in 400 L of lake water (100 L collected at each of four stations). These combined samples were then sent to Stanley Sutey, at Accipiter Fish and Wildlife Services, for enumeration. Cladocera and copepods (adults and copepodids) were identified to the species level. Nauplii were identified only to the sub-ordinal levels. Edmondson (1959) was the principal taxonomic reference, but we followed Brooks (1957) for *Daphnia*, Dussart and Fernando (1990) for Cyclopoida, Korinek (1981) for *Diaphanosoma*, and Lieder (1983) for bosminids. Eggs per female were counted for all species. To calculate biomass, body lengths of all animals were measured using a semi-automated counting and measuring system (Allen et al. 1994). Corrections for contraction due to preservative, were applied to the body length of *Holopedium gibberum* (Yan and Mackie 1987), but not to other species (Campbell and Chow-Fraser 1995). Animal weights were estimated using length-weight regressions summarized in Girard & Reid (1990). If preserved animals were used to develop these regressions, a 39 % correction for weight loss in formalin was applied (Giguère et al. 1989).

Sockeye salmon field assessment: Fish (juvenile sockeye) densities were estimated at night using either a Furuno FM-21, 200 kHz echosounder with 100 W of power output or a Simrad EYM, 70 KHz sounder (Hyatt et al. 1984). On all surveys, pulse width was maintained at 1.0 ms and a varied gain circuit controlled for attenuation losses due to increasing target depth. Surveys were conducted at night using whole-lake transects and several depth strata. The resulting density estimates were used to determine the number of juvenile sockeye found in each lake and to estimate sockeye mortality throughout the late summer, fall and winter periods. Due to fish schooling behaviour, the best estimates were obtained from August through to the pre-smolting period in February. Details regarding transducer design and counting methods are provided in, Hyatt et al. (1984), Gjernes et al. (1986), Hyatt and Stockner (1985). When the Simrad EYM 500 was used to assess fish densities, we were also able to use EP500 v5.5 software produced by Lindem Data Acquisition Ltd. to separate 0+ nerkids from other larger fish. The software uses "indirect statistical methods" (Craig and Forbes 1969) to predict an in-situ target strength (TS) distribution which allowed us to separate fish > 10 cm. In Vernon lake, this was possible on four dates (27 June 2000, 29 Aug 2001, 13 Dec 2001 and 22 June 2003).

Fish biosamples were collected throughout the sampling period using a mid-water trawl net (2 m x 2 m mouth opening x 7.5 m long) (stretch mesh ranging from 5.0 cm at the mouth to 1.3 cm knotless nylon at the cod end). The net was towed only at night, and surveys were based on 5 - 15 trawls per sampling session. The catch included juvenile sockeye and a few (<0.01%) stickleback from Woss Lake and juvenile sockeye and some "other *nerka*" probably kokanee from Vernon Lake. Sampled fish were used to estimate lengths, weights and ages. Using combined data from Woss, Cheewat, Yakoun and Skidegate lakes located in southern British Columbia and Queen Charlotte Islands, K.D. Hyatt (unpublished data) determined that sockeye fry over 40 mm in length begin to swim at speeds that allow them to more easily avoid the trawl net. To correct for this trawl-net size selection, the expression (corrected length = 0.5419 (length in the trawl)$^{1.1965}$) was developed. During March we collected juvenile sockeye from Woss (2002 and 2003) and Vernon Lakes (2002); and the weights of these fish trawled during March were compared to the weights of smolts caught the next month (April-May) of the same years. From these data we developed a Woss Lake trawl correction that was applied to juvenile sockeye in all years. We applied the Woss lake correction to Vernon as well. This correction was applied only to trawl mean lengths > 40 mm and had the effect of gradually increasing "corrected length" as the trawl length increased.

Stomach content samples: Immediately upon capture, juvenile fish destined for stomach-content analysis, were measured (length/weight) and placed into 90% ethanol. At the laboratory these samples were placed in a freezer. During analysis, stomachs were removed, contents washed into a petri dish and all zooplankton counted. The resulting data set included: date, lake, location, depth, fish length/weight, numbers of each zooplankton species. Stomach content data were used to parameterize the fish bioenergetics model (described below), which was used to estimate the numbers of each prey-type consumed by sockeye from each L of lake water per day. The model requires biomass data so it was necessary to convert densities of prey found in fish stomachs to biomasses of each prey-type. Because many of the prey had been damaged during consumption, we estimated individual prey weights from the average weights of each prey type found in the zooplankton samples collected on each sampling date. The biomass of each prey species-type consumed was then calculated by multiplying prey densities per stomach by the mean prey weight. Because sockeye are known to consume larger bodied zooplankton prey (body length >0.5 mm), our use of the average prey weight found in field collections could potentially lead to underestimate the total prey weights consumed. We therefore estimated mean species-specific body weights only from individuals > 0.5 mm in length.

Production and consumption analysis

Zooplankton production: Ultimately the goal of this analysis was to calculate consumption by the fish as a percentage of production by the zooplankton. When consumption exceeded production we expected to see the zooplankton population decline, and at that point we could assume that the "sockeye production capacity" of the lake has been reached or exceeded. Production analysis requires information about zooplankton species composition, biomass, density and egg counts per individual.

Trial production estimates for *D. dentifera* (the most common species found in both lakes) were calculated using two methods. The first method was described in Downing and Rigler (1984), where egg development time is based on the Belehradek equation $K=a(T-\alpha)^b$ where T is temperature and a, α, b are from Cooley et al. (1986). Production is simply calculated as $P = (\beta^*(n_t + n_{t+1})/2)^*w$, where β is number of eggs produced per day, n is numbers per L, and w is mean individual weight ($\mu g\ L^{-1}$ dry weight). The second method was similar to the one used by Borgmann et al. (1984). Egg development time was based on the Belehradek equation $K=a(T-\alpha)^b$ where T is temperature and a, α, b are from Cooley et al. (1986). Production is $P=(N_{t+1}-N_t)(b/r)w$, where b = instantaneous birth rate calculated from Paloheimo (1974) so that $b = \ln(((E_0/N_0)+E_t/N_t))/2+1)k/24$ where E is egg density, N is female density and K is development time in hours, and r is the instantaneous rate of population change from Cooley et al. (1986) and is calculated from $r = (\ln n_t - \ln N_o)/t$ where t is delta time. Trials using both methods gave very similar results, and because Borgmann et al. (1984) argue that method 2 has several technical advantages. Using appropriate (Cooley et al. 1986) parameters for the Belehradek equation, we used method 2 for all cladocerans and copepods. On a sample by sample basis, we then compared species-specific production rates using biomass and egg-count data collected every 3 weeks from the field. For every Δt we compared the potential biomass increase calculated using the production model, with the actual biomass increase observed in the field, and in all cases we selected the larger of the two. This method was applied because at some times of the year, particular species were very rare and egg counts were impossible to obtain.

Fish production and consumption: Calculated rates of zooplankton consumption by 0+ sockeye and 1+ sockeye, were based on bioenergetics models of Kitchell et al. (1974, 1977), summarized in (Hanson et al, 1997). All simulations began on 15 June and ended on 31 October. Model inputs (water temperatures and fish lengths, weights) were measured *in situ* and are reported in the results that follow. Because the Wisconsin model lacks the capacity to simulate diel migration, we approximated a 12 h:12 h migration pattern by alternating daily temperatures between epilimnetic and hypolimnetic values and running the model for twice the required number of days. The validity of this method was tested with a series of diel migration experiments conducted at both lakes on 26-27 June 2000, 6-7 August 2000, and 18-19 August 2003; and it was found that in Woss and Vernon Lakes, the sockeye entered the epilimnion at dark and returned to the hypolimnion at dawn. This meant that the 12:12 h pattern modeled in this study, tended to slightly overestimate food consumption rates, but because summer epilimnetic temperatures in both lakes were low ($13\text{-}17^{O}$) and because the mean day length for the simulation period (June 15 - Oct 31) was about 13.4 hours, the error was small (about 3 %).

Fertilizer loading

The fertilizer added to Woss Lake (see table below), comprised a mix of 28:0:0 and 10:34:0. The mixture 10:34:0 comprises 14.85% P (34% P_2O_5), and 10% N . The mixture 28:0:0 comprises 28% N. During the first three years, the mixture remained the same throughout, having an N:P ratio of 30:1 atomic (13.5:1 mass). During the fourth year, the N:P ratio was increased from 30:1 (April to mid-May) to 40:1 (mid-May to June) to 50:1 (July to August).

Year	kg of P	kg of N	Kg of 10:34:0	Kg of 28:0:0	Total kg of fertilizer
2000	595	8055	4003	27336	31340
2001	730	9890	4916	33567	38483
2002	975	13210	6566	44833	51398
2003	739	13457	4996	46275	51271

RESULTS AND DISCUSSION

NUTRIENT LOADING

Woss Lake was fertilized for four years (2000-03). Vernon Lake was not fertilized and remained the reference lake throughout. With each succeeding year the fertilizer was applied earlier in the year and total quantities added were also increased (Fig. 4). The fertilizers were added twice a week into the eastern and western sections of the lake. Because the fertilizers were added from a boat, we were concerned that they may not have mixed well with the epilimnetic water. This could have resulted in either losses to the hypolimnion or failure to mix laterally across the lake. Therefore in order to assess the extent of fertilizer mixing during year 2000, Gwa'ni Hatchery staff collected phosphorus samples on five dates (July 26, August 2, August 16, August 23, August 30; 2000) from 8 stations (except July 26). Station 1 was at the extreme north end of the lake, Station 8 at the south. Stations 2,3,4 were located on the east, center and west sides of the lake five km from the north end. Stations 5,6,7 were located on the east, center and west sides of the lake five km from the south end. All samples were taken at a depth of 3 m at all stations. In addition, stations 3 and 6 were sampled at 25 m depth. The resulting data (Fig. 5) suggested that the phosphorus mixed completely (concentrations at the center stations (stations 3 and 6) where no higher than the edge stations) and did not fall into the hypolimnion (the deep samples contained less phosphorus than the surface samples). From this we concluded that additions from a boat were reliable and well mixed.

Oxygen and temperature

During all four years in both lakes, epilimnetic oxygen concentrations (Fig. 6) gradually declined from spring highs of approximately 12 mg L^{-1} to late summer lows of approximately 9 mg L^{-1}. During all four years, in both lakes, epilimnetic temperatures (Fig. 7) gradually increased reaching summer highs during late August. Vernon Lake epilimnetic temperatures were consistently lower than Woss Lake temperatures. This was likely due to a substantial snow field in the mountains at the lake head. In both lakes, thermal stratification was generally well established by mid-June and lasted through to mid-October. In both lakes, thermoclines were wide (from approximately 15m to 25m) and Δ temperatures were small (between 0.1 and 0.7 $^{\circ}C\ m^{-1}$.).

Water chemistry

Woss and Vernon Lakes showed different within-year and between-year patterns for spring - fall concentrations of phosphorus (TP), nitrogen (NO_3) and chlorophyll a, (Figs. 8, 9, 10).

Total phosphorus (TP) concentrations in the epilimnion and hypolimnion of both lakes, were about equal (about 4 $\mu g\ L^{-1}$) during the first two years, and tracked well throughout the summer season. However, during the 3rd and 4th years, when the Woss Lake loading rate was increased by approximately 30% (Fig. 4), mid-summer phosphorus concentrations in Woss Lake (fertilized), were somewhat higher than in Vernon Lake (unfertilized). In the case of hypolimnetic concentrations, the trends were similar, except during 2003 when hypolimnetic TP concentrations in Woss Lake increased substantially during August and September. This was associated with shift in the N:P ratio used in Woss Lake and also with a mid-summer bloom of *Rhizosolenia eriensis* (see phytoplankton section). The overall trend (Fig. 11) through the years, was that Woss Lake TP was always 0.5-1.0 $\mu g\ L^{-1}$ greater than in Vernon Lake, and that Vernon Lake TP gradually declined from 2000-02.

The trends in NO_3 concentrations were quite different (Fig. 9). During the first two years, both epilimnetic and hypolimnetic NO_3 concentrations in Woss Lake (unfertilized) were consistently about 10 $\mu g\ L^{-1}$ lower than in Vernon Lake (Figs. 9, 11). During the 3rd year, when loading rates were increased (Table 3), Woss Lake NO_3 declined even more rapidly, so that by the end of the summer, NO_3 concentrations were about 4 $\mu g\ L^{-1}$. During the 4th year, despite the fact that the N:P loading ratio was increased throughout the summer, Woss Lake NO_3 fell rapidly during the second week of June and remained low (< 3 $\mu g\ L^{-1}$) for the remainder of the summer..

Chlorophyll a concentrations in Woss Lake (fertilized) varied substantially from year to year (Fig. 10). During 2000, there was a fall bloom and during 2002, and 2003, blooms appeared in the spring and summer. At Vernon Lake, chlorophyll a concentrations were relatively stable (approximately 0.5 $\mu g\ L^{-1}$) within years and between years (Fig. 10). Vernon Lake chlorophyll concentrations were always lower than Woss Lake chlorophyll concentrations (Fig. 11).

Phytoplankton

Phytoplankton biovolumes ($mm^3\ m^{-3}$) (Fig. 12), had almost exactly the same patterns as chlorophyll a. At Woss Lake, during 2000, both Cyanophyceae and Chlorophyceae were relatively common until the fall when there was a very large

Bacillariophyceae bloom (Table 4). During 2001 at Woss Lake, algal abundances were relatively low with a variety of Bacillariophyceae (*Tabellaria*, *Cyclotella*, *Asterionella*) being the dominant genera at (Tables 4). During 2002 and 2003 blooms again appeared at Woss Lake, this time in the spring and summer, and Bacillariophyceae were again responsible. At Vernon Lake during 2000 and 2001, only Cyanophyceae were relatively common, and no blooms were observed (Table 5). During 2002-03 biovolumes were low and stable (< 200 mm^3 m^{-3}) and blooms were never observed (Fig. 12. Table 5). Overall comparisons between Woss Lake (fertilized) and Vernon Lake (not fertilized) showed that in every year Woss Lake had much higher mean annual (May – October) algal biovolume (Fig. 13).

Two of the three Bacillariophyceae blooms observed in Woss Lake (2000, 2003) were caused by one species; *Rhizosolenia eriensis* (Fig. 14). *R. eriensis* cells resemble large "glass-like" cylinders, measuring approximately 75 x 6 x 4 µm and having spines at each end . This shape ensures that they are non-grazable and it also allows individual cells to absorb considerable quantities of nutrients that might otherwise fuel the growth of grazable species. Clearly the presence of this species created a false impression about the potential significance of fertilizer-induced algal production for energy transfer to zooplankton in Woss Lake.

In addition, *R. eriensis* was not the only large-celled and therefore non-edible genus found in Woss Lake. For each collection date we determined the "edibility" of the genera that were encountered. Our assessment was based on daily mean cell size for each genus, and was also based on digestibility and toxicity (see Methods for details). For each sampling date, all cells were measured and average lengths, widths, and heights were calculated. These measurements were then used to decide whether a particular genus would be included as "edible" or not edible on a particular date. It should be noted that on some dates, cells belonging to particular genus were small enough to be included as edible and on other dates they were excluded based on cell size. The general list of edible algae (Table 6) reflects this, as some normally non-edible genera such as *Rhizosolenia* and *Oscillatoria* are included. For each sampling date, for both lakes, the biovolume of "edible" cells was estimated (Fig. 15), and it is clear that (Figs. 12, 13) edible biovolumes comprised only a fraction of total biovolumes (Fig. 16). At Woss Lake the only real exception was 2002 (Fig. 16), when an edible diatom (a new and undescribed block-shaped species measuring 20 x 8 x 4 µm) bloomed during May and June (dark symbols - Fig. 15). This bloom was repeated during the spring of 2003.

Overall, at Woss Lake (Fig. 16), non-edible algae were always more common than edible algae, suggesting that much of the fertilizer was wasted on species that were nutrient sinks rather than active food web participants. At Vernon Lake, non-edible algae were more abundant only during the first two years (2000-01) and thereafter edible algae were much more abundant. Despite the apparent "waste" of Woss Lake fertilizer (Fig. 17), mean annual comparisons show that Woss Lake always had more edible algae than Vernon Lake, especially during 2003-04 when the unidentified diatom bloomed (Fig. 15).

Zooplankton biomass, densities, egg counts

The Woss Lake pelagic zooplankton community (Table 7) comprised 5 *Daphnia* species with *D. dentifera* being the most common; and three bosminids with *B. longirostris* being the most common. There was only one cyclopoid - *Cyclops bicuspidatus thomasi,* and two calanoids - *Skistodiaptomus oregonensis* and *Epischura navadensis. Holopedium gibberum* was relatively common, and *Polyphemus pediculus* relatively rare. The zooplankton assemblage at Vernon Lake (Table 8) was almost identical except that *Epischura* and *Skistodiaptomus* were absent and *Hesperodiaptomus kenai* was present.

The temporal patterns in both lakes varied considerably (Figs. 18, 19). At Woss Lake (Fig. 18 -), total zooplankton biomasses were lowest during 2000 and highest in the spring of 2002. However, biomasses of *Daphnia* (the best food source for sockeye) were highest during 2000 and 2001. In the later years, they were replaced by *Bosmina*. This was especially true in 2003. In general the overall pattern at Woss Lake, was one of gradually increasing zooplankton biomasses from the early to the later years, and gradual replacement of *Daphnia* by *Bosmina.* At Vernon Lake (Fig. 19), the biomass pattern was almost reversed. The largest biomasses were observed in the early years and gradually became smaller in the later years. Throughout, species compositions remained relatively stable, with *C. b. thomasi* and *B. longirostris* being the most common.

These trends were reflected in the mean annual biomass (Fig. 20) and density (Fig. 21), which showed that Vernon Lake, biomasses and densities were higher in 2000-01 and Woss Lake biomasses and densities were higher in 2002-03. It must be stressed however, that although Woss Lake biomasses were substantially higher during 2003-04, high-quality food species (daphnids) were replaced by lower quality species (bosminids). An important characteristic of zooplankton communities under stress from planktivores is that the mean body sizes of the most vulnerable prey often decline with increased predation pressure. At both Woss (Fig. 22) and Vernon (Fig. 23) Lakes, there were no clear between-year trends. However both *D. dentifera* and *H. gibberum* were consistently larger at Woss Lake than they were at Vernon Lake. This could have been due to between-lake differences in planktivory or perhaps the two lakes had slightly different genotypes.

Egg densities are expected to increase with increased nutrient and algal availability. In both lakes, egg densities were relatively low, but there were exceptions. At Woss Lake during 2002, there was a substantial bloom of a small edible diatom and this was accompanied by increased egg production (Fig. 24, Table 9) and higher zooplankton biomasses (Fig. 18). At Vernon Lake, most species (Fig. 25, Table 10) had more eggs during 2000 when biomasses (Fig. 19) were relatively high. However, during 2001, Vernon Lake spring biomasses were even higher (Fig. 19), but egg counts were low. These trends also apply to brood sizes for egg carrying females. At Woss Lake (Fig. 26), brood sizes tended to be larger during 2002. At Vernon Lake (Fig. 27), there was very little between-year variation in brood sizes. In general, brood sizes were larger at Woss Lake than at Vernon Lake. Overall (Fig. 28), during the first two years of the experiment, average egg densities were higher at Vernon Lake, but during the last two years of the experiment, the trend reversed and Woss egg densities were largest. This was especially true during 2002, when Woss Lake egg densities were about four times larger than during 2001 and 2003.

In both Lakes, cladocerans, especially *Bosmina*, comprised substantial portions of the zooplankton biomass (Figs. 18, 19). However, for short periods of time (weeks), copepods were equally important (Figs. 29, 30). In both lakes the copepod species composition was limited. *C. b. thomasi* was found in both Woss and Vernon Lakes. *S. oregonensis* was found only in Woss and *H. kenai* only in Vernon. *C. b. thomasi* stage IV copepodids emerged from diapause in the spring, metamorphosed into stage V copepodids and adults and produced eggs throughout the summer. They were generally more abundant in Vernon Lake except during 2002, when large numbers were associated with that year's spring edible diatom bloom (Fig. 17) in Woss Lake. Woss Lake *S. oregonensis* were never very abundant. They emerged from overwintering eggs in the spring, metamorphosed through the summer and appeared as large copepodids and adults in the fall. *H. kenai* in Vernon Lake were much more abundant. They appeared as copepodids and adults throughout the summer, especially during 2000; and in most years (Table 10), produced eggs during the late summer and fall. It should be noted that with each succeeding year, Vernon Lake *H. kenai* abundance declined, so that by 2003, they were almost absent from the lake.

Zooplankton production

Species-specific production rates were estimated for each sampling interval (Tables 3) for each lake for each year. At Woss Lake (Fig. 31, Tables 11, 13, 15, 17) during 2000 (Table 11), the most productive species were *H. gibberum* and *Daphnia sp* (primarily *D. dentifera*). During 2001 at Woss Lake, *Bosmina* (primarily *B. longirostris*) and *Daphnia* were most productive (Table 13). During the last two years, *Daphnia* almost disappeared and the highest rates of production came from *Bosmina* and *C. b. thomasi* (Fig. 31, Table 15, 17). At Vernon Lake (Fig. 32; Tables 12, 14, 16, 18), most of the production during the first year (2000) came from the daphnids (primarily *D. dentifera*), and the copepods (*C. b. thomasi* and *H. kenai*) (Table 12). During the second year, (2001) (Table 14) and third (2002) year (Table 16), daphnids were replaced by bosminids and the copepods continued to contribute substantially to overall production rates. During the final year (Table 18) copepod production declined, leaving only *B. longirostris* with relatively high rates of production.

Overall, (Fig. 33, Table 19) during the first two years of the experiment, Vernon Lake (not fertilized) production rates were almost twice the rates observed in Woss Lake (fertilized). However, during the last two years of the experiment, Woss Lake production (and biomass) increased substantially and Vernon Lake production declined. Throughout, daily production rates varied from 0.5 to 1.5 $\mu g\ L^{-1}\ d^{-1}$ (mean 0.7 $\mu g\ L^{-1}\ d^{-1}$)

which is 2.2% of mean biomass. Throughout, seasonal (May-October) P/B ratios averaged 3.7 in Woss Lake and 4.2 in Vernon Lake (Table 19).

Sockeye salmon densities, lengths and weights

At Woss Lake, 21 mid-water trawl and acoustic assessments were made during 2000-03 (Table 20). A total of 1,961 fish were captured, weighed, measured and preserved for stomach content analysis. Length-weight regressions (Fig. 34) showed no between-year variation in condition factor. At Vernon Lake, 18 mid-water trawl and acoustic assessments were made during 2000-03 (Table 20). A total of 1,129 fish were captured, weighed, measured and preserved for stomach content analysis. Length-weight regressions (Fig. 35) showed no between-year variation in weights attained at specific body lengths.

Gear selectivity: Earlier studies showed that sockeye fry over 40 mm in length begin to swim at speeds that allow them to more easily avoid the trawl net towed from a small (4 m) inflatable boats (e.g. Zodiacs and Bombards). To correct for the size bias that results from this type of gear selectivity, (K.D. Hyatt, unpublished data - Pacific Biological Station) juvenile sockeye lengths and weights sampled simultaneously with trawl nets and smolt traps at Cheewat, Yakoun and Skidegate Lakes (located in southern British Columbia and Queen Charlotte Islands), were used to develop a size selectivity correction (corrected length = 0.5419 (length in the trawl)$^{1.1965}$). At both Woss and Vernon Lakes, we checked for possible size biased sampling properties of the same trawl gear towed from a larger power launch. We collected fish in the trawl net during the winter and then compared lengths and weights with fish captured in smolt traps during the early spring (Table 21). At Woss Lake, we found that the smolts were longer and heaver than the trawled juveniles. Although statistically significant, these differences are much less than those predicted by the size-selectivity correction formula noted above. At Vernon Lake, differences between the trawled juveniles and the spring smolts were even smaller. Based on the available Woss Lake data we concluded that size corrections should be applied to fish > 40 mm length. The correction that we used was: corrected length = 0.629*(length in the trawl)$^{1.125}$. Although this correction had a relatively minor effect on mean length (about 4 % increase for trawl-caught fish measuring 70 mm), it was none the less, important for the estimation of population biomass.

In both lakes, most of the trawl catch comprised 0+ juvenile sockeye, but a small number of 1+ sockeye and some larger nerkids (kokanee) were also captured. In Woss Lake during 2000-03, 0.55% (11/2014) of the trawl catch comprised fish that were larger than 0+ sockeye (Table 22, Fig. 36). Nine of these (0.4 %) were kokanee and two were 1+ sockeye. In Vernon lake during 2001-03, 4.8 % (55/1129) of the trawl catch comprised fish that were larger than 0+ sockeye (Table 22, Fig. 37). Forty-four (3.9 %) were kokanee and 11 were 1+ sockeye. In Vernon lake on four dates, we used a Simrad EYM to estimate fish densities, and on those dates we were able to apply target strength analysis to estimate the densities of these larger kokanee. The results showed that during the first year of the study (2000) only 0.3 - 1.2 % of the targets could be attributed to fish > 10 cm, but as the years progressed that number increased from 4.6 - 8.5 % on 29 Aug and 2.8 - 8.8 % on 13 Dec. 2001, to 16.9 % - 24.4 % on 22 June 2003.

0+ Sockeye lengths and weights: Sockeye lengths and weights were monitored several times per year (Table 23) using the mid-water trawl noted above. In both lakes, most growth took place through the spring and early summer, and then began to tail off in the fall (Fig. 38). In all but the first year, Woss Lake (fertilized) growth rates were much higher than Vernon Lake rates (note that in figure 38, 95% confidence intervals are plotted, but are so small that on most dates they are hidden by the symbol). The impression is (Fig. 39) that the fertilization of Woss Lake resulted in higher sockeye growth rates. However, there are two problems with this interpretation. (1) During 2000, growth rates in both lakes were the same, even though Vernon Lake was not fertilized. (2) The divergence between the fertilized lake (Woss) and the unfertilized control (Vernon), was due almost entirely to the fact that growth rates in Vernon Lake declined during 2000-03.

How should these results be interpreted? (1) One interpretation could be that some external factors (such as interannual climate variability) caused reduced growth rates in both lakes, but that Woss Lake was protected by fertilization. (2) Another interpretation is that both lakes had similar production capacities, but that some local event such as increased food consumption by kokanee, resulted in reduced growth rates in Vernon Lake sockeye. In order to determine which of these interpretations is the correct one, it is necessary to compare food consumption by the fish with food availability (i.e. zooplankton biomass and production). That is the objective of one of the next sections (fish production and consumption) of this report. First however, we must review the hypothesis that observed trends in growth rates are due to changes in fish densities.

Nerka densities: Fish densities were estimated using acoustic sampling. The technique is very powerful for pelagic fish but has three caveats. The first is that it does not detect fish in the 0-2 m surface stratum. This results in density underestimation, but the errors are minor and are fully discussed in Hyatt et al. (2000). The second is that fish associated with the substrate are not detected. This means that sockeye assessments cannot be reliably made before mid-June when the juveniles leave the shore and move into the water column. The third caveat, is that the technique does not permit the separation of juvenile sockeye and kokanee. Therefore the density estimates that follow necessarily include both *nerka* groups.

Woss Lake pelagic fish densities in (Table 24, Fig. 40, Fig. 41), varied between 500-1000 ha^{-1} throughout the experiment. There were two notable exceptions. The first was during 2001, when Woss densities were reduced to approximately 200 ha^{-1}, and the second was during 2003, when spring densities were very high (1300 ha^{-1}) and then fell to < 500 ha^{-1} in the fall assessments. Vernon Lake pelagic fish densities in (Table 24, Fig. 41), were more variable. During the first two years, densities varied between 500-600 ha^{-1}, but during the last two years, densities began the year at approximately 1000 ha^{-1}, and then in both years gradually declined to 500 ha^{-1} in 2002 and 300 ha^{-1} in 2003.

Fish diets

Sockeye diet analysis was based on the stomach contents of fish sampled from both lakes 5 times each year (Table 25). Over three years, 810 stomachs were analyzed and the patterns were clear cut. In each lake, fish consumed nine different prey types, but virtually all of the prey consumed came from only four taxonomic groups. In Woss Lake (Fig. 42), *Daphnia* (primarily *D. dentifera*) and *Bosmina* (primarily *B. longirostris*) comprised > 90% of the prey consumed. *E. navadensis* and *C. b. thomasi* were also consumed, but in much smaller quantities. In Vernon Lake, *Daphnia*, *Bosmina* and *H. kenai* were the main prey types. *C. b. thomasi* were also consumed, but in much smaller quantities.

Stomach content data were assessed in order to parameterize the fish bioenergetics model, which was used to estimate the numbers of each prey-type consumed by sockeye from each L of lake water per day. The model requires biomass data so it was necessary to convert densities of prey found in fish stomachs to biomasses of each prey-type. As noted in the methods, many of the prey had been damaged during consumption, so we estimated individual prey weights from the average weights of each prey type > 0.5 mm found in the zooplankton samples collected on each sampling date. In terms of prey biomass consumed (Table 26, Fig. 43), the patterns were similar, except that *E. navadensis* in Woss Lake become slightly more important due to their large size.

Comparing these trends in prey selection with prey availability (Figs. 18, 19) confirms that the preferred prey (*Daphnia* and *Bosmina*) were common in both lakes, especially Woss Lake. However, *C .b. thomasi* was also very common in the zooplankton samples, but seldom appeared in the sockeye diets. Similarly *S. oregonensis*, in Woss Lake was almost never consumed, and both calanoid and cyclopoid nauplii were common in both lakes, but never appeared in the sockeye stomachs. As noted above, the primary prey in Woss Lake were *Daphnia*, *Bosmina* and *Epischura*. The primary prey in Vernon Lake were *Daphnia*, *Bosmina* and *H. kenai.*

Bioenergetics-based estimates of prey consumed by sockeye

Sockeye consumption rates were estimated using the Wisconsin Fish Bioenergetics 3.0 model (Hanson et al. 1997). For each lake, the simulations began on June 15 and ended on October 31. These dates are well within the range over which data were collected. Model inputs included: water temperatures (Fig. 7), fish weights (Fig. 38, Table 23), fish densities (Fig. 40, Table 24) and fish stomach contents (Fig. 42, Table 26). Because the Wisconsin model lacks the capacity to simulate diel migration, we approximated a 12h:12h migration pattern by alternating daily temperatures between epilimnetic and hypolimnetic values.

The bioenergetic model was run separately for each year and for each lake; a total of eight model runs. These outputs are detailed in eight tables (year 2000 - Tables 27 & 28; year 2001- Tables 29 & 30; year 2002 - Tables 31 & 32; year 2003 - Tables 33

& 34). Model output included daily estimates of 0+ sockeye numbers and mean weights (therefore biomasses ha^{-1}), and the output included daily estimates of consumption rates (per ha) for 0+ sockeye feeding on each of the zooplankton species or taxonomic groups included in the sockeye diets. The model also tracked total consumption as a percentage of average individual prey weight, and in every case the 0+ sockeye were shown to begin the season consuming about 10% of their body weight per day and to end the season at 5-6% per day, depending on body size and water temperature. These rates are in agreement with those generally found for larval and juvenile fish. From these data, we were able to determine which prey types were the most "edible" and which prey types were avoided. We were also able to compare daily consumption of each of the major prey types with standing stock biomass for that prey type and with daily production rates for each prey type. The resulting comparisons are expressed as: (1) percentage of mean annual standing stock consumed per day, (2) percent of zooplankton standing stock found on each sampling date that was consumed by 0+ sockeye on each date, and (3) for each individual zooplankton species or taxonomic group we were able to calculate percentage of daily production consumed per day. In the paragraphs that follow, we will: identify the most edible species, review percentages of daily production consumed per day, and finally review the percentages of zooplankton standing stocks consumed per day.

Edible and non-edible zooplankton: Daily consumption as a percentage of zooplankton standing stock (year 2000 - Fig. 44; year 2001 - Fig. 45; year 2001 - Fig. 46; year 2003 - Fig. 47) provided an integrated relative index of preferences for individual prey taxa or species. During year 2000 at Woss Lake, fish consumed *Daphnia* (primarily *D. dentifera*), *Bosmina* (primarily *B. longirostris*), *Epischura*, *Polyphemus* and *Holopedium*. They seldom consumed *C. b. thomasi* adults, *C. b. thomasi* copepodids, *S. oregonensis* adults, and *S. oregonensis* copepodids. They never consumed nauplii. These trends held true even when *C. b. thomasi* and *S. oregonensis* densities were very high. During year 2000 at Vernon Lake, fish consumed *Daphnia* (primarily *D. dentifera*), *Bosmina* (primarily *B. longirostris*), and *H. kenai*. They also consumed small portions of the *C. b. thomasi* adults and copepods. Nauplii were never consumed. *S. oregonensis* were not found in Vernon Lake. During years 2001, 2002 and 2003, the patterns were much the same as in year 2000, except that periodically, a few *C. b. thomasi* appeared in the fish diets. *Polyphemus* and *Holopedium* were seldom found in the diets of fish from both lakes. In general, at Woss Lake, only *Daphnia*, *Bosmina* and the large copepod *Epischura navadensis* were consumed at rates > .01% of standing stock per day. At Vernon Lake, only *Daphnia*, *Bosmina* and the large copepod *Hesperodiaptomus kenai*, were consumed at rates > .01% of standing stock per day.

Percent of zooplankton production consumed per day: Daily consumption as a percentage of daily zooplankton production (year 2000 - Fig. 44; year 2001- Fig. 45; year 2001 - Fig. 46; year 2003 - Fig. 47) yields some information about the potential impacts that 0+ sockeye could have on the population dynamics of individual zooplankton species or taxa. Overall, daily consumption rates seldom exceeded 10% of daily production, suggesting that at the observed densities, 0+ sockeye had very little top-down effect on zooplankton populations. However, inspection of the daily data from both Woss and Vernon Lakes (Tables 27-34) shows that for individual taxa during short periods of the year, consumption did exceed production. For example, at Woss Lake in September 2001, consumption rates on daphnids increased to > 700 % of daily production and this correlates well with observed daphnid biomass declines (Table 35). During 2003, at Woss Lake (Table 35), daily *Daphnia* consumption averaged 129% of daily *Daphnia* production (note scale change in Figure 47), and on some dates consumption was almost 4000% of production. Not surprisingly Woss Lake *Daphnia* biomass remained very low during 2003. During 2003, Woss Lake *Bosmina*, also experienced quite high consumption rates (3 - 56% per day), but because *Bosmina* production was high (the second highest production rates observed over the four year experimental period), biomasses remained high (Fig. 18). At Vernon Lake, during early July 2002, daily consumption equaled almost 5000 % of *Bosmina* production and 145% of *H. kenai* production, and this correlates well with biomass declines for both species during early July. At Vernon Lake during 2003, *Daphnia* had all but disappeared and the fish consumed *Bosmina* and the copepod *H. kenai*. Given that *H. kenai* has a fixed life cycle and fixed rates of production, consumption by sockeye may well have been associated with observed long-term declines in abundance.

Percent of edible zooplankton standing stock (biomass) consumed per day: Bioenergetic production-consumption analysis showed that daily consumption by 0+ fish did exceed taxa-specific zooplankton production rates at certain periods in some lake-years. However, before it can be argued that consumption by 0+ fish could have resulted in significant declines in zooplankton biomass, it must be shown that at least for some periods of time (perhaps 2-3 weeks) daily consumption exceeded zooplankton standing-stock biomass as well as zooplankton production. This was seldom the case (Figs. 48, 49, 50, & 51). During 2000 (Fig. 48), at Woss Lake, as much as 5% of edible prey standing stock was removed (per day) during September, and biomass did decline. However, at other times in the year, percent edible zooplankton standing stock consumed per day was < 1%. At Vernon Lake, daily consumption never exceeded 1% of edible standing stock. During 2001 (Fig. 49), the situation was identical to 2000. During 2002 (Fig. 50), consumption by Vernon Lake 0+ sockeye grew to 2- 4% of edible zooplankton standing stock in the early summer, however for most of the year, daily consumption was < 0.5% of edible zooplankton biomass. During 2002, Woss Lake consumption remained at < 1% of edible zooplankton standing stock. During 2003, consumption in both lakes remained at < 1% of edible zooplankton standing stock (Fig. 51). From this it seems clear that although some species may have been adversely affected by 0+ sockeye over short periods of time, it is very unlikely that consumption by 0+ fish could have accounted for many of the observed declines in zooplankton standing stocks. Apparently the zooplankton were responding to other factors such as seasonal temperatures, seasonal life cycle patterns including copepod diapause, and the influence of invertebrate predators - specifically *C. b. thomasi*, *E. nevadensis* and *H. kenai*.

On the other hand, it should be noted that although consumption by fish may have had little effect on zooplankton population dynamics, the opposite is not necessarily true. It seems reasonable to assume that as edible zooplankton biomasses increase, consumption rates might be expected to increase as well. However, for Woss Lake, where virtually all nerkids were 0+ sockeye, relative consumptions rates (i.e. consumption rates per unit biomass of 0+ sockeye - Fig. 52), did not change. There was more variability when edible zooplankton biomasses were < 40 µg L^{-1}, but even at the highest edible zooplankton biomasses, daily consumption rates remained about average. Perhaps this is not surprising given that the Woss Lake 0+ sockeye always averaged 200-300 prey per fish stomach (Fig. 42). Although this topic is not explored further in this analysis, these results raise interesting questions about how 0+ sockeye in some other lakes (usually interior lakes with large *Daphnia*), manage to gain 2 or more times as much weight as Woss Lake sockeye.

Woss and Vernon Lakes have different food webs

Overall (Fig. 53), in both lakes during all four years, mean annual consumption by 0+ fish averaged 0.2% of the average total zooplankton standing stock, and about 12% of mean daily zooplankton production. From this it seems reasonable to assume that in both lakes during all four years, 0+ fish had sufficient food available and should have grown at similar rates.

But they did not grow at equal rates (Figs. 38, 39). Several factors are implicated. (1) Between-lake and between-year analyses of 0+ growth rates (expressed as weights attained in December of each year – Fig. 39) show that Woss Lake growth rates during 2000 and 2001 were similar, increased in 2002 and then decreased in 2003. In Vernon Lake, December 0+ weights fell significantly from 2000 to 2002, and then recovered slightly during 2003. In summary, between-lake and between-year growth rates changed a great deal. (2) Stomach content data (Table 25, Fig. 42) showed that in Woss Lake, the average number of zooplankton prey (and prey biomass) found per fish stomach, was about constant during 2000 and 2001, then increased during 2002. At Vernon Lake, the average number of prey found in each 0+ fish stomach, declined during each year from 2000-02. (3) In both lakes, average fish densities changed from year to year (Fig. 41). In Woss Lake, densities declined from 2000 to 2001, and then increased during 2002-03. In Vernon Lake, densities increased through 2000-02 then decreased.

Given all of this between-lake and between-year variability one must ask how it is possible for average fish consumption rates to remain at relatively stable percentages of zooplankton biomass and production (Fig. 53). Not surprisingly the answer is that there appears to be a trade-off between: fish densities, fish growth rates and food availability. For both lakes, the relationship between average fish density and 0+ sockeye growth rates (mean weights in December) is negative (Fig. 54 - top). The relationship between biomass of edible zooplankton and 0+ sockeye growth rates (mean weights in December) is positive (Fig. 54 - bottom). Finally the relationship between 0+ sockeye growth rates and the biomass of edible zooplankton per fish, is also positive

(Fig. 55 - top, p = 0.25, r = 0.77). In summary, the key variable that regulates growth rates, seems to be the amount of edible zooplankton available per fish.

However, there is a problem.

The problem is that we have found a negative relationship between fish density and growth rate (Fig. 54 - top). This suggests that greater densities of fish result in higher rates of zooplankton consumption by the fish population, and therefore less zooplankton available per fish. It is true that the bioenergetic analysis showed that daily consumption by 0+ fish exceeded taxa-specific zooplankton production rates for short periods in some lake-years. But from the analysis above we must also conclude that it is very unlikely that consumption by 0+ fish had much effect on zooplankton standing stocks. So how can there be a negative relationship between fish density and 0+ sockeye growth rates? Closer inspection of the relationships described in figures 54 and 55, shows that the observed trends in the data are almost completely due to the Vernon Lake data. At Woss Lake, changes in fish density, or zooplankton biomass or even zooplankton biomass per fish, have very little influence on the observed growth rates of the 0+ fish population (except during 2002 when zooplankton was very abundant and growth rates were slightly higher). At Vernon Lake, however, all three relationships were strong (Fig. 55 - bottom).

Possible effects of kokanee in Vernon Lake

It seems that the two lakes exhibit different relationships between 0+ fish growth rates and food availability. The relationship for Woss Lake is weak and suggests that in all years there was sufficient zooplankton to allow almost maximal growth rates for 0+ fish living in a coastal lake with relatively small-bodied zooplankton. The slight increase in 2002 shows that more zooplankton could improve fish growth, but the gain was relatively small. At Vernon Lake, changes in fish density were negatively correlated with changes in zooplankton abundance (Fig. 56), yet all of the production-consumption analysis has shown that at the densities available in Vernon Lake, 0+ fish could not have strongly influenced zooplankton biomass. This suggests that some of the "fish targets" assessed using acoustics, must have been larger fish that had the capacity to reduce zooplankton biomasses. As noted earlier (Table 22) during 2001-03, larger fish (kokanee) were found in the Vernon Lake trawl nets, and from the acoustic analysis we estimated that 3-24 % of the targets observed at Vernon Lake could have been 1+ , 2+, or 3+ kokanee. It should be noted that kokanee were never observed in Vernon Lake during 2000, and that year stands out (black symbol in Fig. 56) as the one with the highest zooplankton biomasses.

Estimating consumption by Vernon Lake kokanee

To determine the potential effects of various densities of kokanee in Vernon Lake during 2001-02, we ran a series of Vernon Lake bioenergetic analyses using a mix of nerkids including: (1) 100% 0+ sockeye and 0% kokanee, (2) 85 % 0+ sockeye and 15 % kokanee, and (3) 70 % 0+ sockeye and 30 % kokanee. At Vernon lake during 2001, biomasses of zooplankton that were consumed by fish, decreased during July and then gradually increased through the summer (Figs. 19 and 57). Assuming that the fish population comprised 100% 0+ sockeye, the bioenergetics simulation showed that in July, consumption slightly exceeded 1% of biomass, and during the rest of the summer-fall rates fell well below 1%. However, as the percentage kokanee was increased to fifteen percent, total fish consumption increased by a factor of 5 (Fig. 57), and June consumption rates exceeded 5 % of the zooplankton standing stock. When kokanee comprised thirty percent of the fish population, consumption increased 10 fold. At Vernon Lake during 2002 (Fig. 58), biomasses of zooplankton consumed by 0+ fish, increased sharply during June and then declined through the summer. Consumption rates based on the assumption that the fish population comprised 100 % 0+ fish, showed that consumption was never more that 1% of biomass (Fig. 58). However when the kokanee were increased to fifteen percent, total fish consumption more than doubled, and when kokanee comprised thirty percent of the fish population, consumption increased 5 fold. Given the data available, it is impossible to make definitive statements about kokanee densities and the effects of kokanee on Vernon Lake zooplankton, but the preceding suggests that rather limited kokanee populations could have had significant effects on zooplankton standing stocks and could have accounted for the considerably smaller biomasses of edible zooplankton observed in Vernon lake during 2001-02

Top-Down and Bottom-Up relationships

Summaries of mean annual biomasses (Fig. 59), reveal three notable general characteristics: (1) During most years "edible phytoplankton" (Fig. 59 - row 2), comprised < 20% of the total phytoplankton biomass. The other 80 % were either too large (> 30 μm over the longest length-width-height axis), or had gelatinous sheaths. Toxic species were not found in either lake. The notable exception was Woss 2002, when mean annual biomasses of a small edible diatom equaled 50% of the total. (2) During most years in both lakes, zooplankton (Fig. 59 - row 3) eaten by 0+ sockeye (defined here as "edible zooplankton"), equaled about 2/3 of the total zooplankton biomass. In Woss Lake the three edible groups included *Daphnia*, *Bosmina* and *E. nevadensis*. In Vernon Lake the edible groups were *Daphnia*, *Bosmina* and *H. kenai*. Taxa that were seldom selected included, *Polyphemus*, *Holopedium*, *S. oregonensis*, *C. b. thomasi* and all nauplii. (3) On average in Woss Lake, about 20% of the stimulus provided by fertilizers went to edible algae suitable as a food base for zooplankton. Assuming an ecological efficiency of 15 %, about 3 % of the potential biomass stimulated by the addition of fertilizer was converted into total zooplankton biomass. Since edible zooplankton comprised about sixty-eight percent of total zooplankton biomass, the result was that about 2 % of the potential biomass stimulated by the addition of fertilizer comprised edible zooplankton. Putting that another way, it seems likely that in coastal lakes such as Woss and Vernon Lakes, 98 % of fertilizer potential was lost from the food web as it moved from fertilizer to edible zooplankton.

At Woss Lake: Given the above, it is perhaps surprising that during 2002, the observed high 0+ sockeye growth rates were very well correlated with the highest recorded mean annual fertilizer additions (Fig. 59 - top right), edible algal biomasses (Fig. 59 - 2nd row right) and edible zooplankton biomasses (Fig. 59 - 3rd row right). However, during 2000, 2001 and 2003, there was almost no connection. Specifically: (Fig. 59 - black bars only), (1) Woss Lake, total phosphorus (Fig. 59 - top row), declined through to 2002 and then increased slightly in 2003. Woss Lake total algal biovolume (Fig. 59 - 2nd row) was high in 2000, declined in 2001 and then increased from 2001-03. Woss Lake edible algal biovolume (Fig. 59 - 2nd row right) was low in 2001-02, and then much higher in 2002 when there was a bloom of an unidentified edible-sized diatom species. All possible bottom-up correlations between epilimnetic TP and: edible algae, non-edible algae, and chlorophyll a; failed to show the expected bottom-up pattern (see examples in the top two panels of figure 60). However, when edible algal biomass was correlated with kg P loaded as fertilizer per year (Fig. 60 bottom panel), there was a positive relationship driven by the 2002 data point. From this we conclude that during 2000-01 and 2003, the bottom-up link between TP and algae was relatively weak. But, during 2002 there was a very strong bloom of an edible-sized diatom species. This bloom did not correlate with epilimnetic TP but it did correlate with the relatively high rate of P loading that was used in 2002. This species was not seen in earlier years, but did reappear briefly in 2003. (2) Woss Lake zooplankton and edible zooplankton (Fig. 59 - 3rd row) increased from 2000-02 and then declined slightly in 2003. Correlations involving total or edible zooplankton biomass with respect to total phytoplankton biomass or chlorophyll a showed no relationship (an example is given in figure 61- row 1). However, the bottom-up plot of edible zooplankton biomass with respect to edible algal biomass (Fig. 61 - middle row) suggests that higher zooplankton biomasses are associated with higher algal biomasses. Of course this relationship is again driven by 2002 when the edible diatom bloom noted above was observed. Clearly zooplankton responded in a positive way to this exceptional food supply. (3) Woss Lake 0+ sockeye growth rates (December biomasses Fig. 59 - bottom row) increased significantly during 2002 and then declined significantly during 2003. Again year 2002 stands out as an exception having had high biomasses of edible algae, high biomasses of total zooplankton and edible zooplankton, and the highest recorded 0+ sockeye growth rates and December biomasses. However, overall there was no relationship between Woss Lake 0+ sockeye growth rate and edible zooplankton available per fish (Fig. 61 - bottom).

In summary, at Woss Lake, bottom-up energy transfer from fertilizers to fish was efficient during 2002 But, during the other three years, bottom-up transfers from nutrients → algae → zooplankton were not as efficient and this was equally true for energy exchange between edible zooplankton → 0+ sockeye (Fig. 61 - bottom row). It might be noted that although 2002 December 0+ sockeye were significantly larger than the average weight attained in the other three years, the increase was relatively small equaling 8.7 %.

At Vernon Lake: Between-year trends at Vernon Lake were completely different from those observed at Woss. Overall, at the bottom of the food web, there were no density-dependent relationships between nutrients and algae (Fig. 62); but at the top of the food web, more edible zooplankton per fish was strongly associated with higher 0+

sockeye growth rates. Specifically (Fig. 59 - gray bars only): (1) Vernon Lake, total phosphorus (Fig. 59 - top row), decreased through to 2002 and then increased slightly in 2003. Vernon Lake total algal biovolume (Fig. 59 - 2nd row) decreased steadily throughout the four year experiment. Vernon Lake edible algal biovolume (Fig. 59 - 2nd row) was low throughout. All possible bottom-up correlations between epilimnetic TP and: edible algae, inedible algae, and chlorophyll a ; failed to show the expected bottom-up pattern (Fig. 62). (2) Vernon Lake zooplankton and edible zooplankton (Fig. 59 - third row) generally decreased during 2000-03. Correlations involving total zooplankton biomass with respect to total phytoplankton biomass or chlorophyll a showed no relationship (an example is given in figure 63 - row 1). More importantly, the correlation between total zooplankton biomass and edible phytoplankton biomass was negative (Fig. 63- row 2) suggesting top-down regulation. (3) Vernon Lake 0+ sockeye growth rates (December biomasses Fig. 59 – bottom row) decreased significantly from 2000 - 02 and then increased slightly in 2003. Throughout this four year period, there was a strong correlation between 0+ sockeye growth and availability of edible zooplankton (Fig. 63 – bottom). As we have seen from earlier sections of this analysis, 0+ sockeye were not large enough or numerous enough to cause the observed reductions in zooplankton standing stocks, but quite small numbers of larger kokanee could easily have caused the observed trends.

In summary, at Vernon Lake, density dependent patterns of energy transfer from nutrients → algae were not found. Total algal biomass was about equal at all epilimnetic TP concentrations (Figs. 59, 62) and edible algal biomass was negatively associated with epilimnetic TP (Fig. 62 - bottom). At the algae → zooplankton link in the food web, the relationship was negative, suggesting that fewer zooplankton and therefore less grazing pressure, was associated with the production of higher algal standing stocks. At the zooplankton → 0+ sockeye link in the food web, more edible zooplankton were associated with higher sockeye growth rates. It seems likely that when adult kokanee abundances were higher (especially 2001 and 2002), zooplankton biomasses were reduced, and 0+ sockeye growth rates fell. Also, lower zooplankton biomasses were associated with higher phytoplankton biomasses. In other words, this is a good example of a top-down trophic cascade, with kokanee and 0+ sockeye competing for edible zooplankton which were reduced at high kokanee densities, resulting in more algae and reduced sockeye growth.

Comparisons with historical trends

Between 1978 and 1996, two of us, (Hyatt and Rankin - unpublished data) conducted annual fall surveys to Woss Lake that included acoustic and trawl assessments of juvenile sockeye lengths, weights, and densities (Fig. 64). During most of those early years, sockeye densities were markedly higher than during 2000-03, and 0+ sockeye weights were substantially lower, suggesting a top-down density dependent relationship between zooplankton biomass and sockeye growth rates. The 2000-02 Woss Lake data are in almost perfect conformity with these earlier data, suggesting that

Woss Lake fertilization may have had only a modest influence on fall-fry weights when fish densities were low.

Historical data for Vernon Lake are unavailable, but it is interesting to note that the 2000-03 Vernon Lake data (Fig. 64) plot almost directly on the Woss Lake data. This is especially the case for the 2000 data point and also for 2001 (second largest weights). While the data for 2002 and 2003 also generally plot with the Woss data, they are perhaps somewhat lower than expected, again supporting the conclusion that kokanee reduced zooplankton biomasses during those years.

Should Woss Lake fertilization continue?

From a management perspective, the question of interest is "could we stop fertilizing Woss Lake and still get the average 0+ sockeye growth rates that we observed during 2000-03?" The best answer to this question comes from estimates of the quantity of additional 0+ sockeye biomass stimulated by Woss Lake fertilization. To simplify the explanation of calculations used to estimate phosphorus flux through the Woss Lake food web during 2000-03, the following paragraph uses year 2000 as an example. Calculations for the other three years 2001-03 follow the same methods, but results vary considerably from year to year. Details for all of the data summarized in table 8, were provided earlier in the Results section.

In 2000, the amount of fertilizer phosphorus (FP) added to the lake was 436 kg per Lake (Table 36 row-1). During that year (2000), there was a bloom of ungrazable algae and percent edible algae (Table 36 row-2) was very low (5 % of total algal standing stock). Note that in other years percent edible algae was much higher, and this had significant effects on phosphorus dynamics. Assuming 100 % phosphorus uptake and no recycling, 23.9 g ha^{-1} of fertilizer phosphorus (FP) was incorporated into edible algae (i.e. algal cells that could be consumed by zooplankton) (Table 36 row-3). Assuming an edible algae-to-zooplankton ecological efficiency of 15 %, the amount of FP incorporated into total zooplankton was 3.6 g ha^{-1} (Table 36 row-5). Year 2000 percent edible zooplankton (species consumed by 0+ sockeye) was 86 % (Table 36 row-6), so that FP incorporated into edible zooplankton was 3.1 % (Table 36 row-7). Edible zooplankton production was 90 kg ha^{-1} ww (Table 36 row-8). Using a conversion of 0.75% (dw) (Parsons et al. 1984) 96 g ha^{-1} total P was incorporated into zooplankton production (Table 36 row-9). During year 2000, the biomass of edible zooplankton consumed by 0+ sockeye was 13.7 kg ha^{-1} ww (Table 36 row-10), and this determined the amount of total phosphorus (14.6 g ha^{-1}, Table 36 row-11) and FP (0.47 g ha^{-1}, Table 36 row-12) consumed by 0+ sockeye. During 2000, mean sockeye density was 650 ha^{-1} (Table 36 row-13), mean weight gained between June 15 and October 31 was 2.4 g per fish (Table 36 row-14), and 0+ sockeye production was 1589 g ha^{-1} (Table 36 row-15). Using the conversion of 0.35% ww P (Larkin and Slaney 1997) these net production estimates can be converted to total phosphorus (5.6 g ha^{-1}, Table 36 row-16) and FP (0.18 g ha^{-1}, Table 36 row-17) incorporated into new tissue by 0+ sockeye. Finally, the percent of the total phosphorus in 0+ sockeye biomass made up of FP, was

3.18 %. That is, during year 2000, 3.18 % (or 69 kg) of Woss Lake 0+ sockeye production, was stimulated by fertilizer additions (Table 36 row-19).

Earlier we asked whether we "could we stop fertilizing Woss Lake and still get the average 0+ sockeye growth rates that we observed during 2000-03?". The answer is no. During all years Woss Lake fertilization had some benefit, but between-year variability was high. In some years such as year 2000, the benefit was minimal (69 additional kg of 0+ sockeye per lake). In other years the benefit was greater and the extra biomass stimulated by the addition of fertilizer was 114 kg in 2001, 399 kg in 2002 and 206 kg in 2003. On average during 2000-03, fertilizer-P contributed to an additional 200 kg (150 g ha^{-1}) of juvenile sockeye production per year to Woss Lake. At Woss Lake during 2000-03, the mean loading rate was 570 g P ha^{-1} y^{-1} and cost was about CDN \$30 ha^{-1} (fertilizer plus application). This translated to approximately CDN \$200 per kg of enhanced smolt production.

The almost 10-fold variability noted above was regulated mainly by three factors: (1) food web structure in coastal sockeye nursery lakes, (2) year to year changes in percent edible algae and (3) year to year changes in density of the 0+ sockeye.

Coastal nursery lake food web structure has a strong effect on the relative percentages of FP incorporated into algae, zooplankton and fish (Table 37). On average 18 % of the FP was incorporated into edible algae, 2% into edible zooplankton and < 0.10 % into 0+ sockeye (Table 37). As expected, the ratio of algal production to zooplankton production averaged about 10 %. However the ratio between zooplankton production and fish production was much smaller averaging approximately 5 %. In part this was due to low 2000-03 fish densities and the resulting largely unused portions of zooplankton production, but it may also have been due to the structure of pelagic food webs found in coastal sockeye nursery lakes. Many of North Pacific coastal lakes tend to be dominated by a combination of large diatoms that are too large to be consumed by most "grazing" zooplankton, and pico-plankton (Stockner et al. 1987) that are too small. The pico-plankton are known to fuel extensive microbial loops which remineralize nutrients that become available to larger phytoplankton. However, these microbial loops include several trophic conversions with associated losses, and even when remineralized nutrients are taken up by larger algae, the chances are relatively low (average 18% in Woss Lake) that the new cells are edible. In addition, many coastal nursery lakes tend to have simple zooplankton food webs dominated by *Cyclops bicuspidatus thomasi* and *Skistodiaptomus oregonensis*, which are too small and fast to yield much food value to sockeye. Coastal food webs also frequently lack the large *Daphnia* species that are more typical of eutrophic interior nursery lakes. Simply put, the algal cell size distributions and zooplankton species compositions found in coastal nursery lake food webs mitigate against efficient nutrient transfer from fertilizer up through the food web to juvenile sockeye.

The second factor that caused high year to year variability in Woss Lake phosphorus flux and sockeye yields, was percent edible algae. Much of that effect was determined by the presence or absence of *Rhizosolenia eriensis*. For example during

2000, a bloom of *R. eriensis* reduced percent edible algae to about 5 % and this was associated with increased 0+ sockeye yields of only 69 kg ha^{-1}. On the other hand, during year 2002, *Rhizosolenia* were almost absent, small grazable diatoms were common, percent edible algae increased to 48% and 0+ sockeye yields were enhanced by almost 400 kg (per lake year).

The third factor causing year to year variability in sockeye production, is 0+ sockeye density. At Woss Lake, historical sockeye fry densities (Fig. 64) have been 10 times higher than the densities recorded during 2000-03. During those unfertilized years (1980s and 1990s), there was a strong relationship between fry density and fry weight. When densities exceeded 1500 fry ha^{-1}, typical fall-fry weights averaged only 1.0 - 1.5 g and production rates averaged 2 - 4 kg ha^{-1}. In comparison, during the fertilized years, average fry density was only 646 ha^{-1} and the average 0+ sockeye yield was 2.1 kg ha^{-1}. The fairly small differences between these fertilized vs. unfertilized fall-fry weight and yield differences, were due in part to top-down density-dependent effects of higher fry densities on zooplankton biomasses, and in part to the bottom-up effects of fertilization. During the fertilized years (2000-03) about 9.5 % of the phosphorus incorporated into zooplankton came from fertilizers (3.2% in 2000, 8.2 % in 2001, 19.0 % in 2002 and 7.8 %). As we have seen this resulted in fall-fry that were about 9.5 % larger than they would have been without fertilizer additions. The rest of the "production potential", provided by the fertilizer was lost from the system. Some was lost to zooplankton species and molt classes (i.e. *C. b. thomasi, S. oregonensis*, all rotifers, all nauplii) that were not consumed by Woss Lake fry. The rest was lost because during the fertilized years, sockeye densities were so low that large portions of edible zooplankton production could not be consumed by sockeye. On an individual basis, sockeye feeding rates were high and stomachs were full (200 - 300 prey per stomach). But at an average density of 646 fry ha^{-1}, each fry occupied almost 400 m^3 of epilimnetic lake water, which contained almost 3,000,000 edible zooplankton. Small wonder that they had little top-down effect on zooplankton population dynamics and left large portions of fertilizer-induced zooplankton production capacity unused. Based on production-consumption analysis it seems likely that during the fertilized years, fry densities could have been doubled or tripled without affecting the elevated growth rates observed during 2000-03. Briefly stated, if future escapements to Woss Lake remain low, fertilization in combination with stocking will be required for efficient stock rebuilding.

Recommendations

In 2005 and beyond, we recommend renewal of the Woss Lake fertilization program using a new fertilizer mix that will increase phosphorus loading rates from 700 to 1200 g ha^{-1} y^{-1} while leaving nitrogen loading rates at approximately 9000 g ha^{-1} y^{-1}. This new mix would be intended to substantially increase primary production while reducing the chances of *Rhizosolenia* blooms. Also, in order to take advantage of the anticipated increases in primary production, we recommend stocking of at least 2,000,000 sockeye fry from the Gwa'ni Hatchery. Current fry densities result in substantial under-use of available zooplankton production. A three-fold increase in fry densities is predicted to produce a 3-fold increase in smolt production..

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Table 1. Summary of some data provided in the text. The abbreviations N = total nitrogen, P = total phosphorus, Chl a = chlorophyll a , NF = years when not fertilized, F = years when fertilized. Calculation of smolt biomass assumes no mortality from fall - fry to smolt. All of the comparisons involve the same lake "before and after" treatment. The exception is the Woss/Vernon experiment where Woss Lake was fertilized and Vernon Lake an unfertilized reference. Blanks cells indicates no data.

	Area ha	Treatment years		Loading $g\ ha^{-1}\ y^{-1}$		TP $\mu g\ L^{-1}$		Chl a $\mu g\ L^{-1}$		Zoop biomass $mg\ m^{-2}$		Smolt weight g		Smolt biomass $g\ ha^{-1}$	
		NF	F	N	P	NF	F	NF	F	NF	F	NF	F	NF	F
GCL	5100	1969 1974-76	1970-73	5184	1227			7.00	11.00	900	7400	2.78	3.13	6950	5822
Hobiton	360	1984	1980-83	5840	861	2.1	3.2	1.30	2.20						
Kennedy CA	1700	1977, 1985	1978-84	9571	1157	1.5	4.3	0.95	4.70						
Kennedy MA	4700	1977-78 1981-84	1979-80, 1985	5691	613	1.6	2.2	1.14	2.30						
Yakoun	810	1982 1986-98[1]	1983-85	3563	553	1.9	4.0	1.69	3.28			1.12	2.47	2700	1700

Table 1 (cont'd)

	Area ha	Treatment years		Loading g ha^{-1} y^{-1}		TP µg L^{-1}		Chl a µg L^{-1}		Zoop biomass mg m^{-2}		Smolt weight g		Smolt biomass g ha^{-1}	
		NF	F	N	P	NF	F	NF	F	NF	F	NF	F	NF	F
Chilko	18500	1984-86, 89 1994-95	1988, 1990-93	5480	499	2.7	4.1	0.90	1.20	829	1119				
Adams	12900	1986	1997	5040	540			0.87	0.97	590	743	2.64	3.68		
Leisure Lake	110	1982-84	1985-92	31100	3455	5.3	9.0	0.65	3.95	70	600	1.70	3.60	2727	9544
Fraser	1660	1985-87	1988-92	8940	982	6.7	8.0	1.00	1.37	150	300	3.60	5.10		
Coghill	1270	1988-92	1993-96	3161	812	8.0	9.8	0.64	2.05	48	92	1.46	1.48	302	641

Table 1 (cont'd)

	Area ha	Treatment years		Loading g ha^{-1} y^{-1}		TP µg L^{-1}		Chl a µg L^{-1}		Zoop biomass mg m^{-2}		Smolt weight g		Smolt biomass g ha^{-1}	
		NF	F	N	P	NF	F	NF	F	NF	F	NF	F	NF	F
[2]Packers 1 vs. 2	210	1981-83	1984-86	17400	1760	14.7	15.0	1.30	2.00	200	349	5.20	10.40	9523	14285
[2]Packers 1 vs 3	210	1981-83	1987-93	19800	619	14.7	13.0	1.30	2.00	200	200	5.20	3.40	9523	12857
[2]Packers 1 vs 4	210	1981-83	1994-96	3000	480	14.7	9.0	1.30	2.00	200	149	5.20	3.40	9523	12857
Redoubt	1280	1980-83	1984-86	15600	1530			0.76	1.20	100	150	4.00	10.00		
Redfish	615	1992	1995-98	5265	281			0.50	1.00	348	453				

[1] Yakoun Lake: water chemistry comparison only during 1982-83. Fish comparisons from all other years.

[2] Packers Lake limnological data come from Mazumder and Edmundson (2002), while the fish data come from Kyle (1994)

Table 1 (cont'd) Data summary from Stockner and Hyatt (1984) and Shortreed et al. (2001). In each case, mean annual data are provided for one non-fertilized year and one year when the lake was fertilized. The abbreviations N = total nitrogen, P = total phosphorus, Chl a = chlorophyll a, NF = years when not fertilized, F = years when fertilized.

Lake	Area ha	Treatment years		N and P added g ha^{-1} y^{-1}		Chl a µg L^{-1}		Zooplankton biomass mg m^{-2} dw	
		NF	**F**	**N**	**P**	**NF**	**F**	**NF**	**F**
Bonilla	230	1979	1980	18217	2696	1.00	5.40	280	700
Kennedy CA	1700	1977	1978	9094	1982			280	400
Kennedy MA	4700	1978	1979	4268	649			270	400
Curtis	300	1979	1980	6067	900	1.24	4.02	100	150
Long	2100	1981	1982	7143	1048	2.24	2.48	150	350
Morice	9610	1978	1980	3479	527			750	820
Sproat	4100		1985-86	11139	493	0.60	1.08	285	590
Nimpkish	3700		1982-87, 89	3327	730	0.80	1.78	73	260
Devon	180	1979, 1981	1980	6222	944	1.79	4.57	77	108
Lowe	370		1979-82	7980	1169	1.22	1.34	180	815

Table 1 (cont'd) Data summary from Hyatt and Stockner (1985). The abbreviations N = total nitrogen, P = total phosphorus, Chl a = chlorophyll a , NF = years when not fertilized, F = years when fertilized. Calculation of smolt biomass assumes no mortality from fall - fry to smolt.

		Treatment years		Loading rates g ha^{-1} y^{-1}		Age 1 smolt weights (g)		Fall-fry densities ha^{-1}		Smolt biomass ha^{-1}	
Lake	Area ha	**NF**	**F**	N	P	**NF**	**F**	**NF**	**F**	**NF**	**F**
Kennedy CA	1700	1977	1978	9094	1982	1.98	2.55	2025	3260	4010	8313
GCL	5100	1969, 1974 -76	1977-81	4029	716	2.78	4.28	2500	2103	6950	9001
Long	2100	1980-81	1977-79	9710	1946	2.47	2.82	4313	7016	10653	19785
Bonilla	230	1979	1980-81	20891	3196	1.62	2.25	1222	5473	1980	12314
Devon	180	1979, 1981	1980	6222	944	2.62	4.35	2903	2796	7606	12163
Curtis	300	1979	1980-81	10867	1617	1.09	2.78	1589	4287	1732	11918
Kitlope	1260	1978	1979-80	8944	1381	2.14	5.20	310	208	663	1082

Table 2. Proportion (as %) of all resident sockeye fry by Nimpkish Watershed nursery lake. Observations are restricted to years between 1978-2003 for which fry estimates could be generated for each of the four principal sockeye nursery lakes in the Nimpkish watershed.

Lake Survey Year	Nimpkish	Woss	Vernon	Schoen	Sockeye Fry (in millions)
1978	56	30	13	1	2.29
1986	37	43	18	2*	5.13**
1987	39	38	18	5	3.19
1988	41	44	13	2	7.45
1989	73	17	8	1	12.82
1991	23	66	10	1	3.17
1992	23	52	25	0	10.02
1993	47	37	13	2	3.74
1994	45	48	6	2	4.64
1997	52	23	22	3	2.58
2001	40	33	25	2*	1.45**
2002	67	13	18	2*	4.68**
2003	65	12	21	2*	3.15**
All Year Average	46.8	35.1	16.2	1.3	3.84

*Schoen Lake was not surveyed in 1986 or 2001-2003 so an estimate was based on its multiyear average contribution (i.e. 2 %) to the totals in years when all four lakes were surveyed.

** Total abundance values adjusted upwards slightly to account for 2 % average contribution of Schoen Lake to aggregate sockeye production.

Table 3. Woss and Vernon Lake sampling schedule 2000-03.

Woss Lake:

Date	Temp. and Oxygen	Water Chem	Algae	Zoop.	Acoustic	Fish Lengths Weights	Fish Density
16-May-00		☐		☐			
9-Jun-00	☐	☐	☐	☐			
26-Jun-00	☐	☐	☐	☐	☐	☐	☐
18-Jul-00	☐	☐	☐	☐		☐	
7-Aug-00	☐	☐	☐	☐		☐	☐
28-Aug-00		☐	☐	☐			
21-Sep-00	☐	☐	☐	☐	☐	☐	☐
18-Oct-00	☐	☐	☐	☐			☐
12-Dec-00					☐	☐	☐
9-May-01	☐	☐		☐			
1-Jun-01		☐	☐	☐			
18-Jun-01	☐	☐	☐	☐			
10-Jul-01		☐	☐	☐	☐	☐	☐
6-Aug-01	☐	☐	☐	☐	☐	☐	☐
3-Sep-01	☐	☐	☐	☐	☐	☐	☐
11-Sep-01		☐	☐				
23-Sep-01		☐	☐				
24-Oct-01	☐	☐	☐	☐	☐	☐	☐
12-Dec-01	☐			☐	☐	☐	☐
5-Mar-02				☐	☐	☐	☐
6-May-02	☐	☐	☐	☐			
27-May-02	☐	☐	☐	☐			
19-Jun-02		☐	☐	☐	☐	☐	☐
10-Jul-02		☐	☐	☐	☐	☐	☐
30-Jul-02	☐	☐	☐	☐	☐	☐	☐
19-Aug-02		☐	☐	☐	☐	☐	☐
13-Sep-02	☐	☐	☐	☐	☐	☐	☐
23-Sep-02	☐	☐	☐	☐	☐	☐	☐
22-Oct-02			☐				
7-Dec-02	☐		☐	☐	☐	☐	☐
6-Mar-03				☐	☐	☐	☐
21-Apr-03		☐	☐	☐			
19-May-03		☐		☐			
24-Jun-03	[	[	[	[	[	[	[
27-Jul-03	[	[	[	[			
28-Aug-03	[	[	[	[			
17-Sep-03		[		[	[	[	[
4-Nov-03				[	[	[	[
3-Dec-03					[	[	[

Table 3 (cont'd)

Vernon Lake:

Date	Temp. and Oxygen	Water Chem	Algae	Zoop.	Acoustic	Fish Lengths Weights	Fish Density
15-May-00		☐		☐			
9-Jun-00	☐	☐	☐	☐			
27-Jun-00	☐	☐	☐	☐	☐	☐	☐
17-Jul-00	☐	☐	☐	☐		☐	
6-Aug-00	☐	☐	☐	☐		☐	☐
28-Aug-00		☐	☐	☐			
22-Sep-00	☐	☐	☐	☐	☐	☐	☐
8-Nov-00	☐	☐	☐	☐			
13-Dec-00					☐	☐	☐
9-May-01	☐	☐	☐	☐			
1-Jun-01		☐	☐	☐			
18-Jun-01	☐	☐	☐	☐			
9-Jul-01		☐	☐	☐	☐	☐	☐
29-Aug-01	☐	☐	☐	☐	☐	☐	☐
11-Sep-01	☐	☐	☐	☐			
23 Sept-01			☐				
23-Oct-01	☐	☐	☐	☐	☐	☐	☐
13-Dec-01					☐	☐	☐
6-May-02	☐	☐	☐	☐			
27-May-02	☐	☐	☐	☐			
19-Jun-02	☐	☐	☐	☐	☐	☐	☐
10-Jul-02		☐	☐	☐	☐	☐	☐
30-Jul-02		☐	☐	☐	☐	☐	☐
19-Aug-02		☐	☐	☐	☐	☐	☐
11-Sep-02	☐	☐	☐	☐	☐	☐	☐
23-Sep-02	☐	☐	☐	☐	☐	☐	☐
22-Oct-02	☐		☐	☐	☐	☐	☐
7-Dec-02			☐				
19-May-03		☐		☐			
23-Jun-03	☐	☐	☐	☐	☐	☐	☐
22-Jul-03		☐	☐				
28-Aug-03	☐	☐	☐	☐			
29-Oct-03				☐	☐	☐	☐
10-Dec-03					☐	☐	☐

Table 4. Woss Lake phytoplankton biovolume (mm^3 m^{-3})(i.e. cubic microns per ml divided by 1000 = mm^3 m^{-3}). Column abbreviations represent algal divisions: Cyanophyceae, Dinophyceae, Cryptophyceae, Chrysophyceae, Chlorophyceae, Bacillariophyceae.

Date	Cyano	Dino	Crypto	Chryso	Chloro	Bacil	Total
10-Jun-00	1	7	3	29	11	16	65
26-Jun-00	4	5	3	32	36	9	88
18-Jul-00	258	23	5	51	151	9	498
7-Aug-00	13	4	11	161	105	6	300
29-Aug-00	392	39	41	68	60	327	928
23-Sep-00	515	10	13	43	92	2582	3256
18-Oct-00	11	4	6	5	38	6535	6599
10-May-01	0	26	6	33	8	70	143
1-Jun-01	1	25	9	93	15	466	609
18-Jun-01	0	8	5	20	43	484	559
10-Jul-01	0	6	7	68	15	418	515
6-Aug-01	0	2	36	24	21	83	166
4-Sep-01	16	7	15	26	50	256	370
11-Sep-01	7	1	7	47	136	1038	1235
23-Sep-01	64	38	22	19	100	1271	1513
24-Oct-01	64	108	19	37	100	1322	1649
6-May-02	2	73	15	22	10	1246	1368
27-May-02	1	31	5	111	14	2644	2806
19-Jun-02	1	23	5	53	9	3792	3883
10-Jul-02	1	14	4	22	4	1723	1768
30-Jul-02	1	10	29	82	7	1103	1232
19-Aug-02	1	14	9	32	4	1018	1078
13-Sep-02	1	31	40	73	9	939	1093
23-Sep-02	1	49	18	94	14	564	740
22-Oct-02	1	55	22	45	8	496	627
7-Dec-02	1	1	12	7	1	148	170
20-Apr-03	1	17	4	56	2	105	185
24-Jun-03	1	62	2	103	39	5444	5651
27-Jul-03	1	35	2	18	10	6127	6193
28-Aug-03	2	3	3	9	7	147	171

Table 5. Vernon Lake phytoplankton biovolume ($mm^3\ m^{-3}$)(i.e. cubic microns per ml divided by 1000 = $mm^3\ m^{-3}$). Column abbreviations represent algal divisions: Cyanophyceae, Dinophyceae, Cryptophyceae, Chrysophyceae, Chlorophyceae, Bacillariophyceae

Date	Cyano	Dino	Crypto	Chryso	Chloro	Bacil	Total
10-Jun-00	43	1	2	35	5	7	92
27-Jun-00	126	3	4	32	28	10	203
17-Jul-00	576	2	0	4	19	5	606
6-Aug-00	947	3	15	41	36	4	1046
29-Aug-00	1496	13	45	62	15	5	1636
22-Sep-00	472	22	13	16	80	36	640
1-Nov-00	119	4	7	46	39	18	233
9-May-01	35	30	5	86	42	7	206
1-Jun-01	47	84	19	65	16	9	240
18-Jun-01	71	5	5	20	19	5	126
9-Jul-01	114	10	4	25	212	28	393
30-Aug-01	129	15	15	51	158	22	390
11-Sep-01	175	23	14	28	30	24	294
23-Sep-01	183	15	7	25	28	29	286
23-Oct-01	164	15	6	21	26	24	256
6-May-02	1	67	5	54	1	12	140
27-May-02	1	10	3	53	4	109	180
19-Jun-02	1	13	1	41	2	209	267
10-Jul-02	1	30	6	37	4	304	382
30-Jul-02	1	10	2	36	2	130	181
18-Aug-02	1	37	5	33	2	116	194
12-Sep-02	1	6	8	21	4	14	54
23-Sep-02	1	5	7	22	2	14	51
22-Oct-02	1	21	9	43	2	24	100
7-Dec-02	1	14	9	30	2	47	103
23-Jun-03	0	28	2	52	3	109	194
21-Jul-03	0	14	4	16	2	44	80
28-Aug-03	3	17	5	15	3	13	56

Table 6. Woss and Vernon Lake algal genera that were identified on at least one sampling date as being edible by zooplankton. Edibility criteria were based on cell size, digestibility and toxicity (see Methods for details).

CYANOPHYCEAE	CHRYSOPHYCEAE	BACILLARIOPHYCEAE	CHLOROPHYCEAE
Aphanocapsa	Bitrichia	Achnanthes	Actinastrum
Anabaena	Chromulina	Aulacoseira (Melosira)	Arthrodesmus
Chroococcus	Chrysidiastrum	Aulacoseira distans	Chlamydomonas
Gomphosphaeria	Chrysochromulina brev.	Cyclotella	Chlorella
Lyngbya	Chrysochromulina parva	Eunotia	Coccomyxa
Merismopedia	Chrysococcus	Gomphonema	Coelastrum
Rhabdoderma	Chrysolykos	Navicula	Cosmarium
	Chrysophyceae cysts	Rhizosolenia eriensis	Crucigenia
DINOPHYCEAE	Chryso. unident. flagellate	Synedra	Dictyosphaerium
Gymnodinium	Coccomyxa	Tabellaria	Gloeocystis
Oscillatoria	Codonocladium	Diatom, new sp.	Gloeotila
Peridinium	Cryptomonas		Gyromitus
P. inconspicuum	Dinobryon (singles)		Monoraphidium
	Epipyxis		Nephrocytium
CRYPTOPHYCEAE	Kephyrion		Oocystis
Cryptaulax	Mallomonas		Pediastrum
Cryptomonas	Ochromonas		Pedinomonas
Katablepharis	Pleuromastix		Polytoma
Pleuromastix	Pseudokephyrion		Quadrigula
Rhodomonas	Rhizochrysis		Scenedesmus
	Salpingoeca		Tetraedron
	Scourfieldia		Unident. Green
	Spiniferomonas		
	Synura		
	Unidentified Chrysomonads		
	Uroglena		

Table 7. Woss Lake zooplankton biomass (µg L^{-1} dry weight)

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2000																			
15-May-00	0.0	0.0	0.1	2.1	0.0	2.4	0.0	1.0	6.7	0.0	1.5	2.2	0.0	0.3	10.2	0.0	1.1	0.2	**27.9**
09-Jun-00	0.1	0.1	0.0	1.6	0.0	4.4	0.0	0.3	6.3	0.0	0.5	0.4	0.1	0.5	0.0	0.0	0.0	0.1	**14.4**
26-Jun-00	0.0	0.1	0.2	3.8	0.1	6.9	0.0	0.0	6.8	0.0	0.6	0.5	0.1	0.6	0.4	0.0	0.6	0.0	**20.7**
18-Jul-00	0.0	0.3	0.0	2.5	0.3	2.3	0.0	0.0	1.9	0.0	0.0	0.3	0.1	0.3	0.0	0.0	0.3	0.0	**8.4**
07-Aug-00	0.1	0.3	0.0	11.2	0.1	9.8	0.0	0.0	2.6	0.1	0.0	0.4	0.0	0.6	2.1	0.0	0.1	0.0	**27.4**
28-Aug-00	0.1	1.6	0.0	9.7	0.5	4.3	0.1	0.0	0.8	0.0	0.2	0.3	0.1	1.7	0.3	0.0	0.6	0.2	**20.5**
21-Sep-00	0.1	0.0	0.0	1.0	0.0	3.9	0.8	0.0	0.3	0.0	0.8	0.3	0.0	2.0	0.0	0.0	0.1	0.0	**9.4**
18-Oct-00	0.0	0.0	0.0	0.9	0.0	0.7	0.1	0.0	5.7	0.1	0.3	0.0	0.0	1.5	0.2	0.0	0.1	0.0	**9.8**
2001																			
09-May-01	0.0	0.0	0.0	0.1	0.0	0.6	0.0	0.0	3.0	1.1	1.5	2.6	0.0	0.4	0.5	0.0	0.1	0.1	**10.2**
01-Jun-01	0.0	0.0	0.0	1.1	0.0	4.9	0.0	0.0	7.5	6.3	7.1	3.5	0.1	0.4	0.0	0.0	0.2	0.1	**31.3**
18-Jun-01	0.0	0.0	0.0	5.2	0.0	5.1	0.3	0.0	15.5	11.7	8.0	5.5	0.1	0.4	2.4	0.0	0.9	0.1	**55.1**
10-Jul-01	0.1	0.0	0.0	13.3	0.0	3.3	2.8	0.0	8.8	17.6	1.0	0.1	0.0	1.4	0.2	0.0	0.1	0.0	**48.6**
06-Aug-01	0.0	0.0	0.0	23.8	0.0	7.7	0.2	0.0	4.3	6.1	0.9	0.3	0.0	0.6	0.0	0.0	0.3	0.0	**44.2**
03-Sep-01	0.0	0.0	0.0	22.4	0.0	0.8	0.1	0.0	0.0	0.0	1.0	0.3	0.0	2.5	0.5	0.0	1.7	0.0	**29.5**
11-Sep-01	0.0	0.0	0.0	17.2	0.0	0.6	0.1	0.0	0.0	0.0	1.6	0.4	0.0	2.1	0.0	0.0	0.7	0.0	**22.8**
23-Sep-01	0.0	0.0	0.0	5.7	0.0	0.9	0.1	0.0	0.0	0.0	0.8	0.3	0.0	1.1	0.8	0.0	0.3	0.0	**10.2**
24-Oct-01	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.2	1.5	0.9	0.0	0.5	0.0	0.0	0.1	0.3	**4.2**
12-Dec-01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.4	0.0	0.1	0.0	0.0	0.0	0.0	**1.4**

Table 7 (cont'd) -Woss Lake zooplankton biomass (µg L^{-1} dry weight)

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2002																			
6-May-02	0.0	0.0	0.0	0.11	0.0	0.34	0.0	0.0	1.54	1.11	3.84	3.2	0.0	0.38	2.65	0.0	0.14	0.02	**13.3**
27-May-02	0.0	0.0	0.0	0.28	0.0	3.05	0.0	0.0	6.25	2.25	15.7	6.49	0.0	0.16	11.2	0.0	0.12	0.01	**45.5**
18-Jun-02	0.0	0.0	0.0	1.74	0.0	13.5	0.0	0.0	16.8	7.47	17.6	28	0.01	0.0	0.0	0.0	0.0	0.01	**85.2**
9-Jul-02	0.0	0.0	0.0	14.4	0.0	14.5	0.08	0.0	23.1	52	10.5	0.81	0.02	0.15	0.0	0.0	0.0	0.0	**115.7**
30-Jul-02	0.0	0.0	0.0	3.71	0.0	0.16	0.0	0.0	36.9	39.4	0.19	0.03	0.0	0.05	0.61	0.0	0.0	0.0	**81.0**
18-Aug-02	0.0	0.0	0.0	0.14	0.0	0.22	0.0	0.0	18.3	9.29	0.21	0.09	0.0	0.16	0.31	0.0	0.03	0.0	**28.7**
12-Sep-02	0.0	0.0	0.0	5.62	0.0	0.3	0.0	0.0	11.9	6.57	2.74	1.44	0.05	0.22	0.0	0.14	0.01	0.02	**29.0**
23-Sep-02	0.0	0.0	0.0	5.32	0.0	0.03	0.0	0.0	3.23	2.88	6.32	1.62	0.0	0.24	0.17	0.09	0.0	0.0	**19.9**
22-Oct-02	0.0	0.0	0.0	5.96	0.0	4.85	0.0	0.0	4.97	7.02	1.42	0.25	0.0	0.61	0.0	0.0	0.05	0.0	**25.1**
2003																			
6-Mar-03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.7	0.3	0.0	0.0	0.0	**2.8**
20-Apr-03	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.5	0.3	0.0	0.5	0.0	0.0	0.0	0.0	**1.6**
19-May-03	0.0	0.0	0.0	1.3	0.0	8.9	0.0	0.0	0.5	0.1	10.7	6.7	0.0	0.5	0.6	0.0	0.3	0.0	**29.7**
24-Jun-03	0.0	0.0	0.0	0.7	0.0	0.2	0.0	0.0	2.2	1.0	0.3	0.0	0.0	0.8	0.0	0.0	0.0	0.0	**5.3**
27-Jul-03	0.0	0.0	0.0	1.7	0.0	0.7	0.0	0.0	28.5	28.6	3.8	2.2	0.0	0.5	1.7	0.0	0.1	0.0	**67.7**
28-Aug-03	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	19.6	30.6	0.6	0.1	0.0	0.2	0.1	0.0	0.0	0.0	**54.9**
16-Sep-03	0.0	0.0	0.0	0.1	0.0	5.7	0.0	0.0	18.0	13.0	1.2	0.4	0.0	0.6	0.3	0.0	0.1	0.0	**39.5**
5-Nov-03	0.0	0.0	0.0	1.5	0.0	0.1	0.0	0.0	12.5	12.8	6.6	0.0	0.0	0.4	0.9	0.0	0.1	0.0	**34.9**

Table 8. Vernon Lake zooplankton biomass ($\mu g\ L^{-1}$ dry weight)

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2000																			
15-May-00	0.0	0.0	0.0	1.4	0.0	0.5	0.0	0.0	1.1	1.1	0.7	6.4	0.0	0.0	0.0	0.3	6.6	0.2	**18.2**
09-Jun-00	0.0	0.0	0.0	7.5	0.0	1.0	0.0	0.0	8.2	1.5	1.4	8.6	0.0	0.0	0.0	4.5	20.1	0.0	**52.8**
27-Jun-00	0.0	0.0	0.0	4.7	0.0	1.0	0.1	0.0	2.7	0.7	0.2	2.7	0.0	0.0	0.0	5.1	7.9	0.0	**25.2**
17-Jul-00	0.0	0.0	0.0	5.2	0.0	0.8	0.4	0.1	3.4	0.3	0.2	0.1	0.0	0.0	0.0	6.6	0.1	0.0	**17.2**
06-Aug-00	0.3	0.0	0.1	14.8	0.0	1.4	0.3	0.1	11.9	0.9	1.0	2.5	0.0	0.0	0.0	10.4	0.0	0.1	**43.8**
28-Aug-00	0.1	0.0	0.0	25.6	0.0	1.5	1.5	0.0	10.9	2.5	5.0	2.3	0.2	0.0	0.0	16.2	0.1	0.3	**66.3**
22-Sep-00	0.0	0.0	0.0	11.9	0.0	0.1	0.5	0.0	2.7	0.5	1.0	1.0	0.1	0.0	0.0	1.9	0.0	0.0	**19.7**
01-Nov-00	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	2.8	0.4	1.0	0.8	0.1	0.0	0.0	0.0	0.0	0.0	**6.8**
2001																			
09-May-01	0.0	0.0	0.0	0.7	0.0	0.3	0.0	0.0	1.2	4.5	9.7	13.8	0.0	0.0	0.0	0.6	3.4	0.1	**34.4**
01-Jun-01	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.3	0.8	1.3	2.6	0.0	0.0	0.0	0.0	3.7	0.0	**9.6**
18-Jun-01	0.0	0.0	0.0	4.8	0.0	2.6	0.0	0.0	0.6	15.6	36.2	29.9	0.0	0.0	0.0	0.1	5.5	0.2	**95.6**
09-Jul-01	0.0	0.0	0.0	4.7	0.0	0.5	0.1	0.0	3.0	18.6	11.8	7.5	0.0	0.0	0.0	12.8	8.0	0.1	**67.1**
30-Aug-01	0.0	0.0	0.0	10.0	0.0	0.3	0.2	0.0	0.5	4.0	5.9	3.0	0.1	0.0	0.0	4.1	0.3	0.3	**28.7**
11-Sep-01	0.0	0.0	0.0	13.4	0.0	0.3	0.4	0.0	0.3	3.3	6.3	2.9	0.0	0.0	0.0	2.2	0.1	0.2	**29.4**
23-Sep-01	0.0	0.0	0.0	10.4	0.0	0.2	0.5	0.0	0.3	2.4	10.6	7.4	0.0	0.0	0.0	0.4	0.0	0.1	**32.4**
23-Oct-01	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.5	3.4	1.1	4.8	0.0	0.0	0.0	0.0	0.1	0.4	**12.8**

Table 8 (cont'd) Vernon Lake zooplankton biomass (µg L^{-1} dry weight)

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2002																			
6-May-02	0.0	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.5	0.1	3.3	1.3	0.1	0.0	0.0	0.0	2.5	0.2	**8.4**
27-May-02	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.3	7.0	19.4	0.0	0.0	0.0	0.2	0.3	0.0	**27.6**
19-Jun-02	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0	0.1	5.0	20.1	17.8	0.0	0.0	0.0	1.7	15.1	0.0	**60.5**
9-Jul-02	0.0	0.0	0.0	0.4	0.0	0.7	0.0	0.0	0.1	0.2	10.3	2.1	0.0	0.0	0.0	0.4	1.0	0.0	**15.1**
31-Jul-02	0.0	0.0	0.0	1.0	0.0	0.6	0.1	0.0	0.3	1.0	7.0	2.5	0.0	0.0	0.0	1.8	0.2	0.0	**14.5**
17-Aug-02	0.0	0.0	0.0	1.0	0.0	2.6	0.2	0.0		2.5	7.9	5.0	0.0	0.0	0.0	4.7	0.0	0.0	**23.8**
11-Sep-02	0.0	0.0	0.0	4.8	0.0	3.9	0.1	0.0	1.3	7.9	4.4	2.2	0.0	0.0	0.0	3.1	0.3	0.0	**27.9**
22-Sep-02	0.0	0.0	0.0	5.4	0.0	1.1	0.0	0.0	0.8	17.5	2.3	3.5	0.1	0.0	0.0	1.0	0.0	0.1	**31.8**
21-Oct-02	0.0	0.0	0.0	3.6	0.0	0.0	0.1	0.0	2.4	20.2	2.4	2.0	0.1	0.0	0.0	0.7	0.2	0.2	**31.8**
2003																			
19-May-03	0.0	0.0	0.0	0.6	0.0	0.3	0.0	0.0	2.6	1.5	10.2	1.9	0.0	0.0	0.0	0.7	0.0	0.0	**17.8**
23-Jun-03	0.0	0.0	0.0	0.7	0.0	1.0	0.0	0.0	0.2	14.9	2.3	0.8	0.0	0.0	0.0	0.5	0.0	0.0	**20.3**
28-Aug-03	0.0	0.0	0.0	8.2	0.0	1.1	0.1	0.0	7.2	5.2	5.2	2.4	0.0	0.0	0.0	1.7	0.1	0.0	**31.1**

Table 9. Woss Lake eggs L^{-1}

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2000																			
15-May-00				0.110		0.080			0.240		0.630			0.093					**1.2**
09-Jun-00		0.008		0.250	0.030	0.200			0.240										**0.7**
26-Jun-00				0.020	0.015	0.020			0.020		0.215			0.075					**0.4**
18-Jul-00				0.010	0.030	0.090	0.020		0.000		0.060								**0.2**
07-Aug-00		0.010		0.180	0.005	0.160			0.040					0.008					**0.4**
28-Aug-00		0.040				0.060			0.080					0.010					**0.2**
21-Sep-00				0.023		0.075	0.050		0.040										**0.2**
18-Oct-00				0.023			0.013		0.785					0.015					**0.8**
2001																			
09-May-01						0.035			0.125										**0.2**
01-Jun-01						0.040			0.003		0.008								**0.1**
18-Jun-01				0.010		0.020			0.060		0.048								**0.1**
10-Jul-01				0.033		0.080	0.148		0.040		0.015								**0.3**
06-Aug-01											0.003								**0.0**
03-Sep-01				0.008		0.003								0.123					**0.1**
11-Sep-01				0.1			0.03				0.08			0.08					**0.3**
23-Sep-01				0.008							0.038			0.01					**0.1**
24-Oct-01				0.015					0.01		0.243			0.010					**0.3**
12-Dec-01				0.01							0.09								**0.1**

Table 9 (cont'd) Woss Lake eggs L^{-1}

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2002																			
5/6/2002				0.018					0.055		0.108								**0.2**
5/27/2002				0.078		0.203			0.360		1.555			0.030					**2.2**
6/18/2002				0.330		0.815			0.035		0.800								**2.0**
7/9/2002				0.950		1.220			0.013		0.020								**2.2**
7/30/2002				0.025		0.005					0.020								**0.1**
8/18/2002				0.008					0.005										**0.0**
9/12/2002				0.045		0.015			0.055		0.065								**0.2**
9/23/2002				0.088		0.010			0.010		0.348								**0.5**
10/22/2002				0.130		0.053			0.315		0.135								**0.6**
2003																			
3/6/2003																			**0.0**
4/20/2003									0.010		0.003								**0.0**
5/19/2003				0.020		0.013			0.065		0.138								**0.2**
6/24/2003				0.018					0.173										**0.2**
7/27/2003				0.010		0.020			0.240					0.030					**0.3**
8/28/2003									0.030										**0.0**
9/16/2003									0.030										**0.0**
11/5/2003				0.010							0.085								**0.1**

Table 10. Vernon Lake eggs L^{-1}

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2000																			
15-May-00				0.120					0.040		0.193								**0.4**
09-Jun-00				0.213			0.007		0.213							0.053			**0.5**
27-Jun-00				0.160		0.007	0.023		0.080		0.080					0.160			**0.5**
17-Jul-00				0.107			0.070		0.071							0.093			**0.3**
06-Aug-00				0.267		0.013	0.020		0.267							0.240			**0.8**
28-Aug-00				0.266			0.160		0.640							0.560			**1.6**
22-Sep-00				0.023			0.040		0.020		0.040					0.027			**0.1**
01-Nov-00									0.057										**0.1**
2001																			
09-May-01				0.003		0.007			0.013		0.083								**0.1**
01-Jun-01				0.010					0.003		0.003								**0.0**
18-Jun-01				0.013		0.010					0.047								**0.1**
09-Jul-01				0.007			0.003												**0.0**
30-Aug-01				0.020		0.007	0.003				0.073					0.027			**0.1**
11-Sep-01				0.180		0.007	0.027		0.017		0.993					0.087			**1.3**
23-Sep-01				0.050		0.013	0.027				0.987					0.013			**1.1**
23-Oct-01				0.013					0.013		0.077								**0.1**

Table 10 (cont'd) Vernon Lake eggs L^{-1}

Date	*Daphnia spp.*	*Daphnia ambigua*	*Daphnia longiremis*	*Daphnia dentifera*	*Daphnia thorata*	*Holopedium gibberum*	*Polyphemus pediculus*	*Bosmina longispina*	*Bosmina longirostris*	*Bosmina spp.*	*C. b. thomasi*	*Cyclopoid copepodid*	*Cyclopoid nauplius*	*S. oregonesis*	*Epischura nevadensis*	*H. kenai*	*Calanoid copepodid*	*Calanoid nauplius*	**TOTAL**
2002																			
5/6/2002				0.002		0.003			0.023		0.002								**0.0**
5/27/2002				0.017		0.013					0.023								**0.1**
6/19/2002				0.030					0.003		0.021								**0.1**
7/9/2002				0.010		0.053					0.017								**0.1**
7/31/2002				0.040		0.027	0.001		0.003		0.143								**0.2**
8/17/2002				0.033		0.133				0.003	0.377					0.143			**0.7**
9/11/2002				0.027		0.067					0.317					0.083			**0.5**
9/22/2002				0.003		0.030					0.210					0.023			**0.3**
10/21/2002				0.017							0.250								**0.3**
2003																			
19/5/2003									0.16										**0.2**
6/23/2003																			**0.0**
8/28/2003				0.027							0.023					0.027			**0.1**

Table 11. Year 2000: Woss Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
15-May-00	2.1160		0.0000		7.793	
09-Jun-00	1.8550	0.05551	0.0000	0.00000	6.616	0.15621
26-Jun-00	4.1320	0.13394	0.0000	0.00000	6.814	0.09840
18-Jul-00	3.1260	0.02704	0.0320	0.00145	1.946	0.00445
07-Aug-00	11.7150	0.42945	0.0070	0.00213	2.697	0.03755
28-Aug-00	11.9170	0.09364	0.0780	0.00338	0.816	0.08728
21-Sep-00	1.0230	0.04152	0.8150	0.03071	0.359	0.04365
18-Oct-00	0.8980	0.01592	0.0910	0.02466	5.847	0.20326
	4.5978	**0.11386**	**0.1279**	**0.00890**	**4.1110**	**0.09011**

Holopedium		**C.b. thomasi**		**S. oregonensis**		**Epischura**	
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
2.432		3.689		1.427		10.212	
4.446	0.08056	0.893	0.04251	0.492	0.01516	0.000	0.00000
6.915	0.14524	1.133	0.01915	1.125	0.03724	0.364	0.02141
2.272	0.15522	0.315	0.02651	0.645	0.01165	0.020	0.00000
9.783	0.37555	0.390	0.00981	0.722	0.00923	2.073	0.10265
4.324	0.13340	0.472	0.00390	2.384	0.07914	0.273	0.00000
3.907	0.06422	1.164	0.02883	2.128	0.00409	0.000	0.00000
0.729	0.01472	0.372	0.00000	1.620	0.00880	0.213	0.00789
4.3510	**0.13842**	**1.0535**	**0.01867**	**1.3179**	**0.02362**	**1.6444**	**0.01885**

Table 12. Year 2000: Vernon Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
15-May-00	1.4400		0.0000		2.179	
09-Jun-00	7.5310	0.24364	0.0160	0.00064	9.741	0.03422
27-Jun-00	4.7190	0.09054	0.1130	0.00623	3.355	0.03879
17-Jul-00	5.2540	0.07483	0.4080	0.02175	3.801	0.45110
06-Aug-00	15.2050	0.49755	0.3160	0.03130	12.823	0.21882
28-Aug-00	25.6590	0.47518	1.5190	0.05468	13.440	0.10411
22-Sep-00	11.9550	0.06204	0.4570	0.06609	3.244	0.03078
01-Nov-00	1.6320	0.00221	0.0380	0.00429	3.179	0.00000
	9.1744	**0.2066**	**0.3584**	**0.0264**	**6.4703**	**0.1254**

Holopedium		**C.b. thomasi**		**H. Kenai**	
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
0.472		7.034		6.883	
0.962	0.01960	10.020	0.01236	24.546	0.12931
0.988	0.00355	2.955	0.00210	12.996	0.32742
0.788	0.00278	0.256	0.16106	6.695	0.36361
1.401	0.03065	3.477	0.19145	10.443	0.88269
1.473	0.00327	7.306	0.01209	16.354	0.37514
0.068	0.00000	1.963	0.00678	1.886	0.01007
0.010	0.00000	1.823	0.00000	0.044	0.00000
0.7703	**0.0086**	**4.3542**	**0.0551**	**9.9809**	**0.2983**

Table 13. Year 2001: Woss Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
09-May-01	0.1420		0.0000		4.1400	
01-Jun-01	1.1480	0.0437	0.0000	0.0000	13.8290	0.4213
18-Jun-01	5.2120	0.2391	0.2890	0.0170	27.1880	0.7858
10-Jul-01	13.3610	0.3704	2.7960	0.1140	26.4160	0.0329
06-Aug-01	23.8250	0.3876	0.1700	0.0426	10.4390	0.0123
03-Sep-01	22.4010	0.0053	0.1070	0.0000	0.0470	0.0000
11-Sep-01	17.2140	0.0698	0.0890	0.0188	0.0570	0.0013
23-Sep-01	5.7220	0.0310	0.1220	0.0135	0.0540	0.0000
24-Oct-01	0.5900	0.0197	0.0000	0.0000	0.2520	0.0064
	9.9572	**0.14582**	**0.3970**	**0.02574**	**9.1580**	**0.15748**

Holopedium		**C.b. thomasi**		**S. oregonensis**		**Epischura**	
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
0.6290		4.1080		0.5870		0.5140	
4.8910	0.1853	10.6000	0.2823	0.6320	0.0020	0.0000	0.0000
5.0600	0.0221	13.4660	0.1686	1.2550	0.0366	2.4310	0.1430
3.3100	0.0690	1.0160	0.0511	1.5130	0.0117	0.1870	0.0000
7.6880	0.1621	1.1930	0.0098	0.9100	0.0000	0.0000	0.0000
0.8380	0.0098	1.3740	0.0065	4.1700	0.1164	0.5270	0.0188
0.6340	0.0017	1.9620	0.0735	2.8390	0.1034	0.0000	0.0000
0.9490	0.0263	1.1380	0.0463	1.3990	0.0416	0.8090	0.0674
0.0290	0.0000	2.3990	0.0618	0.6530	0.0026	0.0100	0.0000
2.6698	**0.05954**	**4.1396**	**0.08747**	**1.5509**	**0.03929**	**0.4976**	**0.02865**

Table 14. Year 2001: Vernon Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$
09-May-01	0.7260		0.0000		5.7040	
01-Jun-01	0.8250	0.0043	0.0000	0.0000	1.0440	0.0021
18-Jun-01	4.8290	0.2355	0.0000	0.0000	16.1800	0.8904
09-Jul-01	4.7040	0.0045	0.1040	0.0050	21.5970	0.2580
30-Aug-01	9.9610	0.1011	0.2050	0.0047	4.5310	0.0000
11-Sep-01	13.4400	0.2899	0.4000	0.0188	3.5340	0.0061
23-Sep-01	10.3770	0.0500	0.5360	0.0301	2.6560	0.0038
23-Oct-01	2.4030	0.0157	0.0230	0.0045	3.9040	0.0416
	5.9081	**0.1001**	**0.1585**	**0.0090**	**7.3938**	**0.1717**

Holopedium		**C.b. thomasi**		**H. Kenai**	
Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$
0.2730		23.4920		4.0380	
0.0220	0.0008	3.9280	0.0087	3.7240	0.0000
2.6200	0.1528	66.0960	3.6569	5.6410	0.1128
0.5170	0.0024	19.2600	0.0086	20.7940	0.7216
0.3370	0.0051	8.9080	0.0480	4.4080	0.2057
0.3060	0.0075	9.2410	0.2972	2.2270	0.2888
0.2420	0.0101	17.9980	0.7298	0.4290	0.1226
0.0470	0.0026	5.8770	0.1181	0.1340	0.0064
0.5455	**0.0259**	**19.3500**	**0.6953**	**5.1744**	**0.2083**

Table 15. Year 2002: Woss Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
6-May-02	0.109		0.000		2.647	
27-May-02	0.283	0.0180	0.000	0.0000	8.493	0.2784
18-Jun-02	1.742	0.1053	0.000	0.0000	24.246	0.7160
9-Jul-02	14.436	0.6045	0.078	0.0037	75.166	2.4248
30-Jul-02	3.714	0.2301	0.000	0.0000	76.254	0.0518
18-Aug-02	0.135	0.0218	0.000	0.0000	27.548	0.0064
12-Sep-02	5.618	0.2193	0.000	0.0000	18.462	0.0409
23-Sep-02	5.318	0.0710	0.000	0.0000	6.104	0.0254
22-Oct-02	5.956	0.0885	0.000	0.0000	11.993	0.2031
	4.1457	**0.16980**	**0.0087**	**0.00046**	**27.8792**	**0.46834**

Holopedium		**C.b. thomasi**		**S. oregonensis**		**Epischura**	
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
0.338		7.038		0.525		2.653	
3.049	0.1291	22.191	0.7216	0.278	0.0145	11.183	0.4062
13.528	0.4763	45.675	1.0675	0.000	0.0000		0.0000
14.466	1.6450	11.357	0.2115	0.147	0.0070		0.0000
0.157	0.2791	0.221	0.1000	0.045	0.0000	0.612	0.0291
0.220	0.0067	0.295	0.0111	0.193	0.0078	0.312	0.0000
0.300	0.0116	4.183	0.1555	0.229	0.0014		0.0000
0.032	0.0079	7.938	0.3414	0.239	0.0009	0.171	0.0155
4.850	0.1661	1.668	0.2466	0.662	0.0146		0.0000
4.1044	**0.34025**	**11.1740**	**0.35687**	**0.2576**	**0.00578**	**2.9862**	**0.05636**

Table 16. Year 2002: Vernon Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}
6-May-02	0.116		0.000		0.582	
27-May-02	0.144	0.0017	0.000	0.0000	0.433	0.0048
19-Jun-02	0.350	0.0090	0.000	0.0000	5.111	0.2034
9-Jul-02	0.373	0.0081	0.008	0.0004	0.292	0.0003
31-Jul-02	1.044	0.0305	0.073	0.0030	1.340	0.0476
17-Aug-02	0.986	0.0144	0.181	0.0064	2.465	0.0662
11-Sep-02	4.774	0.1515	0.097	0.0000	9.185	0.2688
22-Sep-02	5.444	0.0609	0.000	0.0000	18.234	0.8226
21-Oct-02	3.628	0.0074	0.065	0.0022	22.557	0.1491
	1.8732	**0.0354**	**0.0471**	**0.0015**	**6.6888**	**0.1954**

Holopedium		**C.b. thomasi**		**H. Kenai**	
Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}
0.285		4.622		2.474	
0.135	0.0026	26.395	1.0368	0.517	0.0000
0.248	0.0049	37.936	0.5018	16.827	0.7091
0.666	0.0209	12.362	0.0161	1.389	0.0000
0.595	0.0148	9.491	0.0636	1.931	0.0246
2.566	0.1159	12.862	0.1994	4.659	0.2338
3.877	0.0551	6.620	0.2022	3.366	0.4299
1.106	0.0437	5.835	0.1505	0.989	0.2517
0.016	0.0024	4.353	0.1509	0.872	0.0610
1.0549	**0.0325**	**13.3862**	**0.2902**	**3.6693**	**0.2138**

Table 17. Year 2003: Woss Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
20-Apr-03	0.058		0.000		0.104	
19-May-03	1.278	0.0031	0.000	0.0000	0.639	0.0184
24-Jun-03	0.713	0.0451	0.000	0.0000	3.256	0.0795
27-Jul-03	1.729	0.0338	0.000	0.0000	57.105	1.6318
28-Aug-03	0.018	0.0556	0.000	0.0000	50.153	0.1129
16-Sep-03	0.092	0.0009	0.000	0.0000	30.990	0.0373
5-Nov-03	1.475	0.0034	0.000	0.0000	25.301	0.0109
	0.7661	**0.02367**	**0.0000**	**0.00000**	**23.9354**	**0.31515**

Holopedium		**C.b. thomasi**		**S. oregonensis**		**Epischura**	
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
0.090		0.801		0.570			
8.938	0.3051	17.388	0.5720	0.776	0.0071	0.606	0.0209
0.219	0.0465	0.335	0.0000	0.766	0.0262		0.0000
0.720	0.0164	6.006	0.1718	0.516	0.0237	1.657	0.0502
3.666	0.0921	0.770	0.0000	0.196	0.0000	0.058	0.0000
5.664	0.1052	1.653	0.0465	0.764	0.0299	0.339	0.0148
0.103	0.0000	6.590	0.0987	0.502	0.0000	0.940	0.0120
2.7714	**0.09421**	**4.7919**	**0.14817**	**0.5843**	**0.01449**	**0.7200**	**0.01632**

Table 18. Year 2003: Vernon Lake biomass and production summary. Biomass is the biomass measured on each sampling date. Production per day is the mean daily production for the interval between the pervious date and the current date. The bold number at the bottom of the biomass column is the mean biomass measured during the spring-fall sampling interval. The bold number at the bottom the of the production column is the mean daily rate of production for the entire spring-fall sampling interval.

	Daphnia		**Polyphemus**		**Bosmina**	
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
19-May-03	0.622		0.000		4.113	
23-Jun-03	0.722	0.0020	0.000	0.0000	15.037	0.2229
28-Aug-03	8.219	0.1136	0.123	0.0019	12.350	0.0000
	3.1877	**0.0578**	**0.0410**	**0.0009**	**10.5000**	**0.1115**

Holopedium		**C.b. thomasi**		**H. Kenai**	
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}
0.253		12.112		0.683	
1.004	0.0153	3.081	0.0000	0.501	0.0000
1.073	0.0010	7.576	0.0681	1.790	0.0409
0.7767	**0.0082**	**7.5897**	**0.0341**	**0.9913**	**0.0205**

Table 19. Biomass and production summary for Woss and Vernon Lakes. Mean production is calculated as production per L per day (dry weight). Seasonal P:B ratio is calculated as summed production during the sampling season (May-October) divided by the average biomass found through the sampling season.

Woss Lake

Year	Length of sampling season	Mean biomass µg L^{-1}	Total seasonal production µg L^{-1}	Seasonal P:B
2000	156	17.2	61.70	3.6
2001	168	28.3	88.40	3.1
2002	169	50.5	239.90	4.8
2003	199	33.6	116.60	3.5

Vernon Lake

Year	Length of sampling season	Mean biomass µg L^{-1}	Total seasonal production µg L^{-1}	Seasonal P:B
2000	170	31.1	133.4	4.3
2001	167	38.5	154.1	4.0
2002	139	26.1	112.9	4.3
2003	115	23.1	26.6	1.2

Table 20. Sockeye trawl-net sampling

Year	Lake	Number of sampling periods	Number of fish sampled
2000	Woss	5	376
2001	Woss	4	305
2002	Woss	8	811
2003	Woss	4	469
2000	Vernon	5	277
2001	Vernon	3	189
2002	Vernon	7	441
2003	Vernon	3	222

Table 21. Comparison of juvenile sockeye trawl-caught length and weights with smolt lengths and weights

		Gear	Date	Length (mm)	95% CI	Weight (g)	95% CI	Sample size
Woss	Juvenile	Trawl	12-Dec-01	67.1	0.7	2.79	0.09	171
Woss	Juvenile	Trawl	20-Feb-02	68.2	1.6	2.76	0.22	53
Woss	Smolt	Trap	6-May-02	71.7	0.9	3.02	0.10	63
Woss	juvenile	Trawl	6-Dec-02	68.4	0.8	3.09	0.11	108
Woss	juvenile	Trawl	5-Mar-03	70.5	0.8	3.31	0.12	124
Woss	Smolt	Trap	April-May 2003	76.0	0.1	3.70	0.47	591
Vernon	Juvenile	Trawl	13-Dec-01	63.0	1.0	2.14	0.08	75
Vernon	Smolt	Trap	15-May-02	64.0	0.7	2.21	0.09	242

Table 22. Total numbers of kokanee captured during trawl-net sampling

Year	Lake	Number 0+ sockeye caught	Number 1+ sockeye caught	Mean 1+ sockeye weight g	Number kokanee caught	Mean kokanee weight g
2000	Woss	376	0	-	0	
2001	Woss	357	1	11.2	0	
2002	Woss	808	0	-	3	66.7
2003	Woss	462	1	6.1	6	47.1
2000	Vernon	277	0	-	0	-
2001	Vernon	165	0	-	24	29.1
2002	Vernon	423	5	4.9	13	25.8
2003	Vernon	209	6	1.2	7	20.3

Table 23. Summary of lengths and weights for 0+ sockeye salmon from Woss and Vernon Lakes.

Date	Lake	N	Mean Length	Mean weight	Length Std Dev.	Weight St Dev	Length 95% CI	Weight 95% CI
26-Jun-2000	Woss	144	40.9	0.7	4.2	0.24	0.69	0.04
18-Jul-2000	Woss	51	48.6	1.3	4.1	0.33	1.13	0.09
07-Aug-2000	Woss	72	54.3	1.7	6.3	0.50	1.46	0.11
21-Sep-2000	Woss	57	62.1	2.4	5.3	0.60	1.37	0.15
12-Dec-2000	Woss	52	64.9	2.8	4.0	0.55	1.09	0.15
27-Jun-2000	Vernon	119	43.4	0.8	4.87	0.30	0.87	0.05
17-Jul-2000	Vernon	51	48.2	1.2	6.1	0.46	1.66	0.13
06-Aug-2000	Vernon	17	55.2	1.7	6.9	0.56	3.27	0.26
22-Sep-2000	Vernon	63	67.7	3.0	4.0	0.55	0.98	0.14
13-Dec-2000	Vernon	27	68.2	2.8	6.7	0.79	2.54	0.30
10-Jul-2001	Woss	31	50.1	1.3	4.6	0.43	1.63	0.15
06-Aug-2001	Woss	80	64.6	2.7	6.1	0.72	1.34	0.16
24-Oct-2001	Woss	22	64.5	2.9	5.5	0.67	2.28	0.28
12-Dec-2001	Woss	171	67.1	2.8	4.6	0.61	0.68	0.09
20-Feb-2002	Woss	53	68.2	2.8	5.8	0.82	1.57	0.22
29-Aug-2001	Vernon	58	58.7	2.0	4.8	0.46	1.23	0.12
23-Oct-2001	Vernon	32	66.6	2.5	6.0	0.52	2.07	0.18
13-Dec-2001	Vernon	75	63.0	2.1	4.0	0.36	0.91	0.08
18-Jun-2002	Woss	31	50.1	1.3	4.6	0.4	1.63	0.15
11-Jul-2002	Woss	120	47.5	1.4	4.1	0.4	0.73	0.07
29-Jul-2002	Woss	139	58.8	2.1	6.0	0.67	0.99	0.11
18-Aug-2002	Woss	150	64.0	2.7	5.2	0.7	0.82	0.12
23-Sep-2002	Woss	113	67.3	2.8	4.5	0.6	0.84	0.11
22-Oct-2002	Woss	23	68.0	3.3	2.3	0.4	0.93	0.17
06-Dec-2002	Woss	108	68.4	3.1	4.2	0.6	0.80	0.11
05-Mar-2003	Woss	124	70.5	3.3	4.4	0.7	0.78	0.12
18-Jun-2002	Vernon	89	37.1	0.4	3.9	0.16	0.80	0.03
09-Jul-2002	Vernon	88	37.0	0.4	3.9	0.16	0.81	0.03
29-Jul-2002	Vernon	109	45.9	0.9	3.4	0.2	0.63	0.04
17-Aug-2002	Vernon	86	50.9	1.8	3.8	0.2	0.79	0.05
22-Sep-2002	Vernon	18	52.1	1.6	4.3	0.3	1.99	0.15
21-Oct-2002	Vernon	28	53.3	1.6	3.8	0.3	1.40	0.11
07-Dec-2002	Vernon	5	53.4	1.4	3.8	0.3	3.37	0.27

Table 23 (cont'd)

Date	Lake	N	Mean Length	Mean weight	Length Std Dev.	Weight St Dev	Length 95% CI	Weight 95% CI
23-Jun-2003	Woss	74	40.9	0.6	4.0	0.2	0.91	0.05
16-Sep-2003	Woss	200	58.6	2.3	4.5	0.5	0.63	0.07
04-Nov-2003	Woss	67	62.9	2.6	4.8	0.6	1.14	0.15
16-Dec-2003	Woss	121	62.4	2.3	4.0	0.5	0.71	0.08
23-Jun-2003	Vernon	102	39.8	0.6	5.2	0.3	1.01	0.06
29-Oct-2003	Vernon	45	54.4	1.6	3.1	0.2	0.91	0.06
10-Dec-2003	Vernon	62	54.6	1.5	3.5	0.3	0.88	0.07

Table 24. Fish densities in Woss and Vernon lakes.

Date	Lake	Density (fish ha^{-1})	95% C.I.	Total abundance (fish $lake^{-1}$)	95% C.I.
26-Jun-2000	Woss	665	418	858,515	539,500
07-Aug-2000	Woss	501	253	646,791	326,295
21-Sep-2000	Woss	477	122	615,807	158,043
18-Oct-2000	Woss	766	223	988,906	287,490
13-Dec-2000	Woss	535	147	690,685	189,575
27-Jun-2000	Vernon	902	403	730,620	326,663
07-Aug-2000	Vernon	441	309	357,210	250,142
22-Sep-2000	Vernon	568	226	460,080	183,363
13-Dec-2000	Vernon	485	126	392,850	102,113
10-Jul-2001	Woss	253	111	327,058	142,980
06-Aug-2001	Woss	362	288	467,684	372,107
03-Sep-2001	Woss	488	299	629,602	385,483
24-Oct-2001	Woss	351	95	453,040	123,127
12-Dec-2001	Woss	202	91	261,123	116,979
09-Jul-2001	Vernon	640	472	518,021	382,544
29-Aug-2001	Vernon	497	442	402,496	358,369
23-Oct-2001	Vernon	550	138	445,166	111,619
13-Dec-2001	Vernon	597	169	483,942	136,915
18-Jun-2002	Woss	624	316	805,846	407,354

Table 24 (cont'd)

Date	Lake	Density (fish ha^{-1})	95% C.I.	Total abundance (fish lake^{-1})	95% C.I.
11-Jul-2002	Woss	840	462	1,083,923	596,851
30-Jul-2002	Woss	614	290	792,552	374,146
18-Aug-2002	Woss	510	285	658,102	368,157
12-Sep-2002	Woss	895	402	1,155,982	518,728
23-Sep-2002	Woss	546	304	704,774	392,006
22-Oct-2002	Woss	639	187	825,346	242,050
05-Mar-2003	Woss	843	264	1,087,675	341,087
18-Jun-2002	Vernon	1,069	474	865,809	383,659
09-Jul-2002	Vernon	1,092	286	884,799	231,898
29-Jul-2002	Vernon	1,018	318	824,795	257,588
17-Aug-2002	Vernon	1,003	398	812,219	322,699
11-Sep-2002	Vernon	974	349	789,301	282,849
21-Sep-2002	Vernon	848	325	686,760	263,384
21-Oct-2002	Vernon	747	262	605,428	212,373
23-Jun-2003	Woss	1,305	441	1,684,281	569,432
16-Sep-2003	Woss	449	215	579,526	277,315
04-Nov-2003	Woss	595	98	768,393	126,379
17-Dec-2003	Woss	514	66	663,548	85,604
22-Jun-2003	Vernon	1,076	632	871,436	511,916
29-Oct-2003	Vernon	524	79	424,750	63,697
10-Dec-2003	Vernon	391	38	316,408	30,875

Table 25. Mean number of prey per fish stomach

		Number of fish counted	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	Calanoids	Calanoid nauplii	*Epischura nevadensis*	*C. b. thomasi*	Cyclopoid nauplii	Diptera	Chironomid larvae	*Chydorus*
Woss	26-Jun-00	30	171.93	0.07	0.00	101.17	0.07	0.00	1.40	0.20	0.00	0.00	0.10	0.00
Woss	18-Jul-00	30	264.67	12.43	1.33	67.13	0.10	0.00	0.03	0.13	0.00	0.03	0.63	0.00
Woss	7-Aug-00	30	321.77	0.57	0.53	11.40	0.00	0.00	11.20	0.00	0.00	0.00	0.10	0.00
Woss	21-Sep-00	30	74.60	3.03	7.47	39.03	0.00	0.00	0.13	0.00	0.00	0.70	0.00	0.03
Woss	12-Dec-00	30	2.30	0.03	0.00	1.67	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
Vernon	27-Jun-00	30	61.40	0.10	0.43	306.20	26.53	0.00	0.00	0.93	0.00	0.00	0.10	0.00
Vernon	17-Jul-00	30	63.90	0.00	0.00	78.13	117.20	0.00	0.00	8.43	0.00	0.03	0.00	0.00
Vernon	6-Aug-00	30	16.87	0.00	0.00	1.13	230.20	0.00	0.00	0.00	0.00	0.43	0.00	0.00
Vernon	22-Sep-00	30	345.47	0.00	0.17	150.57	15.80	0.00	0.00	0.17	0.00	0.00	0.00	0.10
Vernon	13-Dec-00	27	0.11	0.00	0.00	44.22	0.00	0.00	0.00	0.19	0.00	0.00	0.00	0.00

Table 25 (cont'd)

		Number of fish counted	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	Calanoids	Calanoid nauplii	*Epischura nevadensis*	*C. b. thomasi*	Cyclopoid nauplii	Diptera	Chironomid larvae	*Chydorus*
Woss	10-Jul-01	30	101.60	0.13	2.03	72.60	0.00	0.00	0.00	2.17	0.00	0.03	0.03	0.03
Woss	6-Aug-01	30	300.07	0.00	0.70	41.00	0.00	0.00	0.20	1.07	0.00	0.00	0.00	0.03
Woss	3-Sep-01	21	550.67	0.05	0.05	0.00	0.00	0.00	0.10	0.19	0.00	0.00	0.00	0.00
Woss	26-Oct-01	20	40.60	0.00	0.10	6.90	0.00	0.00	4.40	11.55	0.00	0.30	0.05	0.00
Woss	13-Dec-01	30	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vernon	9-Jul-01	27	8.44	0.00	0.07	76.07	36.07	0.00	0.00	35.56	0.00	0.00	0.00	0.00
Vernon	29-Aug-01	10	491.10	1.20	1.00	17.80	139.70	0.00	0.00	0.30	0.00	0.20	0.00	0.00
Vernon	4-Sep-01	30	26.47	0.13	0.17	3.33	208.20	0.00	0.00	0.13	0.00	0.03	0.00	0.00
Vernon	23-Oct-01	30	114.20	0.00	0.07	149.27	0.00	0.00	0.00	18.37	0.00	0.13	0.00	0.00
Vernon	12-Dec-01	30	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00
Woss	30-Jul-02	30	27.73	0.03	0.07	524.27	0.13	0.00	0.00	0.13	0.00	0.07	0.00	0.00
Woss	12-Sep-02	28	334.75	0.00	0.04	183.14	0.00	0.00	0.00	0.32	0.00	0.82	0.00	0.00
Woss	23-Sep-02	30	111.83	0.00	0.00	21.10	0.00	0.00	0.03	2.57	0.00	0.33	0.00	0.00
Woss	23-Oct-02	23	131.48	1.22	0.09	8.04	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00
Woss	6-Dec-02	30	0.07	0.00	0.00	0.73	0.00	0.00	0.03	0.13	0.00	0.00	0.00	0.00

Table 25 (cont'd)

		Number of fish counted	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	Calanoids	Calanoid nauplii	*Epischura nevadensis*	*C. b. thomasi*	Cyclopoid nauplii	Diptera	Chironomid larvae	*Chydorus*
Vernon	19-Jun-02	26	0.08	0.00	0.04	144.00	2.88	0.00	0.00	1.19	0.00	0.12	0.08	0.00
Vernon	29-Jul-02	23	6.35	0.00	0.09	4.57	62.83	0.00	0.00	1.96	0.00	0.00	0.00	0.00
Vernon	10-Sep-02	21	88.67	1.52	1.33	18.81	126.33	0.00	0.00	0.43	0.00	0.05	0.05	0.00
Vernon	22-Sep-02	17	140.06	0.12	0.18	71.47	96.06	0.00	0.00	1.71	0.00	0.18	0.00	0.00
Vernon	22-Oct-02	27	160.70	0.00	0.00	83.41	3.48	0.00	0.00	0.44	0.00	0.04	0.00	0.00

Table 26. Mean percentage prey type per fish stomach. Data are listed as percentages.

		Number of fish counted	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	Calanoids	Calanoid nauplii	*Epischura nevadensis*	*C. b. thomasi*	Cyclopoid nauplii	Diptera	Chironomid larvae	*Chydorus*
Woss	26-Jun-00	30	65.84	0.02	0.00	31.96	0.02	0.00	1.96	0.05	0.00	0.00	0.15	0.00
Woss	18-Jul-00	30	80.42	5.01	0.38	13.75	0.02	0.00	0.02	0.03	0.00	0.00	0.38	0.00
Woss	7-Aug-00	30	83.52	0.18	0.05	2.96	0.00	0.00	13.23	0.00	0.00	0.00	0.06	0.00
Woss	21-Sep-00	30	56.39	2.29	4.17	26.69	0.00	0.00	0.33	0.00	0.00	10.13	0.00	0.00
Woss	12-Dec-00	30	34.71	0.57	0.00	25.83	0.00	0.00	0.00	0.00	0.00	38.89	0.00	0.00
Vernon	27-Jun-00	30	15.45	0.04	0.12	62.15	21.76	0.00	0.00	0.22	0.00	0.00	0.26	0.00
Vernon	17-Jul-00	30	12.59	0.00	0.00	10.92	75.21	0.00	0.00	1.29	0.00	0.00	0.00	0.00
Vernon	6-Aug-00	30	1.57	0.00	0.00	0.09	97.02	0.00	0.00	0.00	0.00	1.31	0.00	0.00
Vernon	22-Sep-00	30	63.78	0.00	0.04	24.53	11.58	0.00	0.00	0.02	0.00	0.00	0.00	0.04
Vernon	13-Dec-00	27	0.19	0.00	0.00	99.54	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00

Table 26 (cont'd)

		Number of fish counted	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	Calanoids	Calanoid nauplii	*Epischura nevadensis*	*C. b. thomasi*	Cyclopoid nauplii	Diptera	Chironomid larvae	*Chydorus*
Woss	10-Jul-01	30	45.00	0.10	1.87	51.60	0.00	0.00	0.00	1.43	0.00	0.00	0.00	0.00
Woss	6-Aug-01	30	80.75	0.00	0.42	18.39	0.00	0.00	0.00	0.44	0.00	0.00	0.00	0.00
Woss	3-Sep-01	21	99.81	0.01	0.01	0.00	0.00	0.00	0.13	0.04	0.00	0.00	0.00	0.00
Woss	26-Oct-01	20	42.57	0.00	0.00	11.07	0.00	0.00	33.25	13.11	0.00	0.00	0.00	0.00
Woss	13-Dec-01	30	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vernon	9-Jul-01	27	1.61	0.00	0.05	25.85	60.98	0.00	0.00	11.52	0.00	0.00	0.00	0.00
Vernon	29-Aug-01	10	26.83	0.12	0.11	1.75	71.16	0.00	0.00	0.03	0.00		0.00	0.00
Vernon	4-Sep-01	30	1.39	0.01	0.00	0.30	98.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vernon	23-Oct-01	30	32.60	0.00	0.04	63.87	0.00	0.00	0.00	3.49	0.00		0.00	0.00
Vernon	12-Dec-01	30	0.00	0.00	0.00	81.84	0.00	0.00	0.00	18.16	0.00	0.00	0.00	0.00
Woss	30-Jul-02	30	5.42	0.01	0.02	94.43	0.07	0.00	0.00	0.04	0.00	0.00	0.00	0.00
Woss	12-Sep-02	28	63.98	0.00	0.01	35.89	0.00	0.00	0.00	0.08	0.00	0.03	0.00	0.00
Woss	23-Sep-02	30	84.22	0.00	0.00	12.77	0.00	0.00	0.23	2.73	0.00	0.05	0.00	0.00
Woss	23-Oct-02	23	92.95	0.93	0.10	4.32	0.00	0.00	1.69	0.00	0.00	0.00	0.00	0.00
Woss	6-Dec-02	30	5.81	0.00	0.00	48.59	0.00	0.00	26.66	18.94	0.00	0.00	0.00	0.00

Table 26 (cont'd)

		Number of fish counted	*Daphnia*	*Holopedium*	*Polyphemus*	*Bosmina*	Calanoids	Calanoid nauplii	*Epischura nevadensis*	*C. b. thomasi*	Cyclopoid nauplii	Diptera	Chironomid larvae	*Chydorus*
Vernon	19-Jun-02	26	0.06	0.00	0.02	86.02	12.57	0.00	0.00	1.30	0.00	0.02	0.00	0.00
Vernon	29-Jul-02	23	0.54	0.00	0.00	0.64	98.36	0.00	0.00	0.47	0.00	0.00	0.00	0.00
Vernon	10-Sep-02	21	3.75	0.11	0.20	1.09	94.80	0.00	0.00	0.04	0.00	0.00	0.00	0.00
Vernon	22-Sep-02	17	10.03	0.01	0.03	4.72	85.02	0.00	0.00	0.18	0.00	0.00	0.00	0.00
Vernon	22-Oct-02	27	56.05	0.00	0.00	31.60	12.11	0.00	0.00	0.24	0.00	0.00	0.00	0.00

Table 27. Year 2000, Woss Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Woss 2000 156 days	**Daphnia**			**Polyphemus**			**Bosmina**		
Date	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}
15-May-00	2.1160			0.0000			7.793		
09-Jun-00	1.8550	0.0555		0.0000	0.00000		6.616	0.15621	
26-Jun-00	4.1320	0.1339	0.0227	0.0000	0.00000	0.00000	6.814	0.09840	0.00850
18-Jul-00	3.1260	0.0270	0.0321	0.0320	0.00145	0.00000	1.946	0.00445	0.00600
07-Aug-00	11.7150	0.4295	0.0394	0.0070	0.00213	0.00000	2.697	0.03755	0.00140
28-Aug-00	11.9170	0.0936	0.0456	0.0780	0.00338	0.00120	0.816	0.08728	0.00940
21-Sep-00	1.0230	0.0415	0.0402	0.8150	0.03071	0.00290	0.359	0.04365	0.02010
18-Oct-00	0.8980	0.0159	0.0292	0.0910	0.02466	0.00090	5.847	0.20326	0.01810
	4.5978	**0.11386**	**0.0350**	**0.1279**	**0.00890**	**0.00080**	**4.1110**	**0.09011**	**0.00130**

	Holopedium			**C.b. thomasi**			**S. oregonensis**			**Epischura**		
	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumpti by fish μg L^{-1} d^{-1}
15-May-00	2.432			3.689			1.427			10.212		
09-Jun-00	4.446	0.08056		0.893	0.04251		0.492	0.01516		0.000	0.00000	
26-Jun-00	6.915	0.14524	0.00050	1.133	0.01915	0.00000	1.125	0.03724	0.00000	0.364	0.02141	0.0004
18-Jul-00	2.272	0.15522	0.00200	0.315	0.02651	0.00000	0.645	0.01165	0.00000	0.020	0.00000	0.0000
07-Aug-00	9.783	0.37555	0.00000	0.390	0.00981	0.00000	0.722	0.00923	0.00000	2.073	0.10265	0.0061
28-Aug-00	4.324	0.13340	0.00060	0.472	0.00390	0.00000	2.384	0.07914	0.00000	0.273	0.00000	0.0045
21-Sep-00	3.907	0.06422	0.00140	1.164	0.02883	0.00000	2.128	0.00409	0.00000	0.000	0.00000	0.0000
18-Oct-00	0.729	0.01472	0.00090	0.372	0.00000	0.00000	1.620	0.00880	0.00000	0.213	0.00789	0.0000
	4.3510	**0.13842**	**0.00090**	**1.0535**	**0.01867**	**0.00000**	**1.3179**	**0.02362**	**0.00000**	**1.6444**	**0.01885**	**0.0017**

Table 28. Year 2000, Vernon Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Vernon 2000

170	**Daphnia**			**Polyphemus**			**Bosmina**		
Date	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}
15-May-00	1.4400			0.0000			2.179		
09-Jun-00	7.5310	0.24364		0.0160	0.00064		9.741	0.03422	
27-Jun-00	4.7190	0.09054	0.00630	0.1130	0.00623	0.00000	3.355	0.03879	0.01920
17-Jul-00	5.2540	0.07483	0.00640	0.4080	0.02175	0.00000	3.801	0.45110	0.00540
06-Aug-00	15.2050	0.49755	0.00100	0.3160	0.03130	0.00000	12.823	0.21882	0.00000
28-Aug-00	25.6590	0.47518	0.01640	1.5190	0.05468	0.00000	13.440	0.10411	0.00630
22-Sep-00	11.9550	0.06204	0.03000	0.4570	0.06609	0.00000	3.244	0.03078	0.01190
01-Nov-00	1.6320	0.00221	0.00000	0.0380	0.00429	0.00000	3.179	0.00000	0.05500
	9.1744	**0.2066**	**0.0120**	**0.3584**	**0.0264**	**0.0000**	**6.4703**	**0.1254**	**0.0151**

Holopedium			**C.b. thomasi**			**H. Kenai**		
Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L^{-1} d^{-1}
0.472			7.034			6.883		
0.962	0.01960		10.020	0.01236		24.546	0.12931	
0.988	0.00355	0.00000	2.955	0.00210	0.00020	12.996	0.32742	0.01850
0.788	0.00278	0.00000	0.256	0.16106	0.00050	6.695	0.36361	0.03680
1.401	0.03065	0.00000	3.477	0.19145	0.00000	10.443	0.88269	0.05060
1.473	0.00327	0.00000	7.306	0.01209	0.00000	16.354	0.37514	0.03080
0.068	0.00000	0.00000	1.963	0.00678	0.00000	1.886	0.01007	0.00570
0.010	0.00000	0.00000	1.823	0.00000	0.00000	0.044	0.00000	0.00000
0.7703	**0.0086**	**0.0000**	**4.3542**	**0.0551**	**0.0001**	**9.9809**	**0.2983**	**0.0207**

Table 29. Year 2001, Woss Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Woss 2001

	Daphnia			**Polyphemus**			**Bosmina**		
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
09-May-01	0.1420			0.0000			4.1400		
01-Jun-01	1.1480	0.0437		0.0000	0.0000		13.8290	0.4213	
18-Jun-01	5.2120	0.2391	0.0111	0.2890	0.0170	0.0004	27.1880	0.7858	0.0118
10-Jul-01	13.3610	0.3704	0.0167	2.7960	0.1140	0.0003	26.4160	0.0329	0.0097
06-Aug-01	23.8250	0.3876	0.0301	0.1700	0.0426	0.0000	10.4390	0.0123	0.0064
03-Sep-01	22.4010	0.0053	0.0381	0.1070	0.0000	0.0000	0.0470	0.0000	0.0001
11-Sep-01	17.2140	0.0698	0.0359	0.0890	0.0188	0.0000	0.0570	0.0013	0.0007
23-Sep-01	5.7220	0.0310	0.0321	0.1220	0.0135	0.0000	0.0540	0.0000	0.0016
24-Oct-01	0.5900	0.0197	0.0192	0.0000	0.0000	0.0000	0.2520	0.0064	0.0038
	9.9572	**0.14582**	**0.02460**	**0.3970**	**0.02574**	**0.00010**	**9.1580**	**0.15748**	**0.00540**

Holopedium			**C.b. thomasi**			**S. oregonensis**			**Epischura**		
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
0.6290			4.1080			0.5870			0.5140		
4.8910	0.1853		10.6000	0.2823		0.6320	0.0020		0.0000	0.0000	
5.0600	0.0221	0.0000	13.4660	0.1686	0.0002	1.2550	0.0366	0.0000	2.4310	0.1430	0
3.3100	0.0690	0.0000	1.0160	0.0511	0.0001	1.5130	0.0117	0.0000	0.1870	0.0000	0
7.6880	0.1621	0.0000	1.1930	0.0098		0.9100	0.0000	0.0000	0.0000	0.0000	0
0.8380	0.0098	0.0000	1.3740	0.0065	0.0002	4.1700	0.1164	0.0000	0.5270	0.0188	0.0004
0.6340	0.0017	0.0000	1.9620	0.0735	0.0009	2.8390	0.1034	0.0000	0.0000	0.0000	0.0022
0.9490	0.0263	0.0000	1.1380	0.0463	0.0019	1.3990	0.0416	0.0000	0.8090	0.0674	0.0049
0.0290	0.0000	0.0000	2.3990	0.0618	0.0044	0.6530	0.0026	0.0000	0.0100	0.0000	0.0113
2.6698	**0.05954**	**0.00000**	**4.1396**	**0.08747**	**0.00120**	**1.5509**	**0.03929**	**0.00000**	**0.4976**	**0.02865**	**0.0029**

Table 30. Year 2001, Vernon Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Vernon 2001

	Daphnia			**Polyphemus**			**Bosmina**		
Date	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L-1 d-1	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L-1 d-1	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L-1 d-1
09-May-01	0.7260			0.0000			5.7040		
01-Jun-01	0.8250	0.0043		0.0000	0.0000		1.0440	0.0021	
18-Jun-01	4.8290	0.2355	0.0020	0.0000	0.0000	0.0000	16.1800	0.8904	0.00750
09-Jul-01	4.7040	0.0045	0.0046	0.1040	0.0050	0.0000	21.5970	0.2580	0.00570
30-Aug-01	9.9610	0.1011	0.0074	0.2050	0.0047	0.0000	4.5310	0.0000	0.00360
11-Sep-01	13.4400	0.2899	0.0107	0.4000	0.0188	0.0000	3.5340	0.0061	0.00090
23-Sep-01	10.3770	0.0500	0.0044	0.5360	0.0301	0.0000	2.6560	0.0038	0.00710
23-Oct-01	2.4030	0.0157	0.0142	0.0230	0.0045	0.0000	3.9040	0.0416	0.02750
	5.9081	**0.1001**	**0.0059**	**0.1585**	**0.0090**	**0.0000**	**7.3938**	**0.1717**	**0.0078**

Holopedium			**C.b. thomasi**			**H. Kenai**		
Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L-1 d-1	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L-1 d-1	Biomass μg L^{-1}	Production μg L^{-1} d^{-1}	Consumption by fish μg L-1 d-1
0.2730			23.4920			4.0380		
0.0220	0.0008		3.9280	0.0087		3.7240	0.0000	
2.6200	0.1528	0.0000	66.0960	3.6569	0.0034	5.6410	0.1128	0.02090
0.5170	0.0024	0.0000	19.2600	0.0086	0.0025	20.7940	0.7216	0.02360
0.3370	0.0051	0.0000	8.9080	0.0480	0.0014	4.4080	0.2057	0.02600
0.3060	0.0075	0.0000	9.2410	0.2972	0.0001	2.2270	0.2888	0.02840
0.2420	0.0101	0.0000	17.9980	0.7298	0.0003	0.4290	0.1226	0.02330
0.0470	0.0026	0.0000	5.8770	0.1181	0.0013	0.1340	0.0064	0.00000
0.5455	**0.0259**	**0.0000**	**19.3500**	**0.6953**	**0.0013**	**5.1744**	**0.2083**	**0.0211**

Table 31. Year 2002, Woss Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Woss 2002

	Daphnia			**Polyphemus**			**Bosmina**		
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
6-May-02	0.109			0.000			2.647		
27-May-02	0.283	0.0180		0.000	0.0000		8.493	0.2784	
18-Jun-02	1.742	0.1053	0.0032	0.000	0.0000	0.0000	24.246	0.7160	0.0369
9-Jul-02	14.436	0.6045	0.0118	0.078	0.0037	0.0000	75.166	2.4248	0.0428
30-Jul-02	3.714	0.2301	0.0187	0.000	0.0000	0.0000	76.254	0.0518	0.0343
18-Aug-02	0.135	0.0218	0.0329	0.000	0.0000	0.0000	27.548	0.0064	0.0361
12-Sep-02	5.618	0.2193	0.0397	0.000	0.0000	0.0000	18.462	0.0409	0.0223
23-Sep-02	5.318	0.0710	0.0651	0.000	0.0000	0.0000	6.104	0.0254	0.0101
22-Oct-02	5.956	0.0885	0.0668	0.000	0.0000	0.0000	11.993	0.2031	0.0045
	4.1457	**0.1698**	**0.0366**	**0.0087**	**0.0005**	**0.0000**	**27.8792**	**0.4683**	**0.0261**

Holopedium			**C.b. thomasi**			**S. oregonensis**			**Epischura**		
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
0.338			7.038			0.525			2.653		
3.049	0.1291		22.191	0.7216		0.278	0.0145		11.183	0.4062	
13.528	0.4763	0.0000	45.675	1.0675	0.0000	0.000	0.0000	0.0000		0.0000	0.0000
14.466	1.6450	0.0000	11.357	0.2115	0.0000	0.147	0.0070	0.0000		0.0000	0.0000
0.157	0.2791	0.0000	0.221	0.1000	0.0000	0.045	0.0000	0.0000	0.612	0.0291	0.0000
0.220	0.0067	0.0000	0.295	0.0111	0.0000	0.193	0.0078	0.0000	0.312	0.0000	0.0000
0.300	0.0116	0.0000	4.183	0.1555	0.0000	0.229	0.0014	0.0000		0.0000	0.0000
0.032	0.0079	0.0000	7.938	0.3414	0.0023	0.239	0.0009	0.0000	0.171	0.0155	0.0000
4.850	0.1661	0.0006	1.668	0.2466	0.0005	0.662	0.0146	0.0000		0.0000	0.0011
4.1044	**0.34025**	**0.00010**	**11.1740**	**0.35687**	**0.0004**	**0.2576**	**0.00578**	**0.00000**	**2.9862**	**0.05636**	**0.0004**

Table 32. Year 2002, Vernon Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Vernon 2002

	Daphnia			**Polyphemus**			**Bosmina**		
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
6-May-02	0.116			0.000			0.582		
27-May-02	0.144	0.0017		0.000	0.0000		0.433	0.0048	
19-Jun-02	0.350	0.0090	0.0000	0.000	0.0000	0.0000	5.111	0.2034	0.02160
9-Jul-02	0.373	0.0081	0.0002	0.008	0.0004	0.0000	0.292	0.0003	0.01320
31-Jul-02	1.044	0.0305	0.0004	0.073	0.0030	0.0000	1.340	0.0476	0.00040
17-Aug-02	0.986	0.0144	0.0008	0.181	0.0064	0.0000	2.465	0.0662	0.00040
11-Sep-02	4.774	0.1515	0.0020	0.097	0.0000	0.0000	9.185	0.2688	0.00060
22-Sep-02	5.444	0.0609	0.0041	0.000	0.0000	0.0000	18.234	0.8226	0.00200
21-Oct-02	3.628	0.0074	0.0228	0.065	0.0022	0.0000	22.557	0.1491	0.01290
	1.8732	**0.0354**	**0.0051**	**0.0471**	**0.0015**	**0.0000**	**6.6888**	**0.1954**	**0.0068**

Holopedium			**C.b. thomasi**			**H. Kenai**		
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
0.285			4.622			2.474		
0.135	0.0026		26.395	1.0368		0.517	0.0000	
0.248	0.0049	0.0000	37.936	0.5018	0.0000	16.827	0.7091	0.00570
0.666	0.0209	0.0000	12.362	0.0161	0.0000	1.389	0.0000	0.02980
0.595	0.0148	0.0000	9.491	0.0636	0.0000	1.931	0.0246	0.03560
2.566	0.1159	0.0000	12.862	0.1994	0.0000	4.659	0.2338	0.03430
3.877	0.0551	0.0000	6.620	0.2022	0.0000	3.366	0.4299	0.04290
1.106	0.0437	0.0000	5.835	0.1505	0.0000	0.989	0.2517	0.03480
0.016	0.0024	0.0000	4.353	0.1509	0.0000	0.872	0.0610	0.01580
1.0549	**0.0325**	**0.0000**	**13.3862**	**0.2902**	**0.0000**	**3.6693**	**0.2138**	**0.0269**

Table 33. Year 2003, Woss Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Woss
2003

	Daphnia			**Polyphemus**			**Bosmina**		
Date	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
20-Apr-03	0.058			0.000			0.104		
19-May-03	1.278	0.0031		0.000	0.0000		0.639	0.0184	
24-Jun-03	0.713	0.0451	0.0060	0.000	0.0000	0.0000	3.256	0.0795	0.0444
27-Jul-03	1.729	0.0338	0.0219	0.000	0.0000	0.0000	57.105	1.6318	0.0437
28-Aug-03	0.018	0.0556	0.0354	0.000	0.0000	0.0000	50.153	0.1129	0.0299
16-Sep-03	0.092	0.0009	0.0375	0.000	0.0000	0.0000	30.990	0.0373	0.0145
5-Nov-03	1.475	0.0034	0.0556	0.000	0.0000	0.0000	25.301	0.0109	0.0024
	0.7661	**0.0237**	**0.0305**	**0.0000**	**0.0000**	**0.0000**	**23.9354**	**0.3151**	**0.0268**

Holopedium			**C.b. thomasi**			**S. oregonensis**			**Epischura**		
Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1	Biomass µg L^{-1}	Production µg L^{-1} d^{-1}	Consumption by fish µg L-1 d-1
0.090			0.801			0.570					
8.938	0.3051		17.388	0.5720		0.776	0.0071		0.606	0.0209	
0.219	0.0465	0.0000	0.335	0.0000	0.0000	0.766	0.0262	0.0000		0.0000	0.0000
0.720	0.0164	0.0000	6.006	0.1718	0.0000	0.516	0.0237	0.0000	1.657	0.0502	0.0000
3.666	0.0921	0.0000	0.770	0.0000	0.0000	0.196	0.0000	0.0000	0.058	0.0000	0.0000
5.664	0.1052	0.0000	1.653	0.0465	0.0000	0.764	0.0299	0.0000	0.339	0.0148	0.0000
0.103	0.0000	0.0006	6.590	0.0987	0.0000	0.502	0.0000	0.0000	0.940	0.0120	0.0012
2.7714	**0.0942**	**0.0001**	**4.7919**	**0.1482**	**0.0000**	**0.5843**	**0.0145**	**0.0000**	**0.7200**	**0.0163**	**0.0002**

Table 34. Year 2003, Vernon Lake daily fish consumption with respect to zooplankton biomass and production Bold-face numbers at the bottom of each column are column averages.

Vernon 2003

	Daphnia			Polyphemus			Bosmina		
Date	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Consumption by fish µg L-1 d-1	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Consumption by fish µg L-1 d-1	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Consumption by fish µg L-1 d-1
5-May-03	0.622			0.000			4.113		
23-Jun-03	0.722	0.0020	0.0001	0.000	0.0000	0.0000	15.037	0.2229	0.02000
28-Aug-03	8.219	0.1136	0.0009	0.123	0.0019	0.0000	12.350	0.0000	0.00030
	3.1877	**0.0578**	**0.0027**	**0.0410**	**0.0009**	**0.0000**	**10.5000**	**0.1115**	**0.0057**

Holopedium			C.b. thomasi			H. Kenai		
Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Consumption by fish µg L-1 d-1	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Consumption by fish µg L-1 d-1	Biomass $\mu g\ L^{-1}$	Production $\mu g\ L^{-1}\ d^{-1}$	Consumption by fish µg L-1 d-1
0.253			12.112			0.683		
1.004	0.0153	0.0000	3.081	0.0000	0.0002	0.501	0.0000	0.00880
1.073	0.0010	0.0000	7.576	0.0681	0.0000	1.790	0.0409	0.02870
0.7767	**0.0082**	**0.0000**	**7.5897**	**0.0341**	**0.0001**	**0.9913**	**0.0205**	**0.01930**

Table 35. Periods during which rates of daily consumption by 0+ fish exceeded daily rates of production by specific zooplankton species. C = consumption µg L^{-1} d^{-1}, and P = production µg L^{-1} d^{-1}.

Lake	Year	Mid-summer	Fall	Reference
Woss	2000	July 18, daphnid & bosminid C/P > 100%	Daphnid C/P almost 200%	Fig 18, Table 27
Woss	2001		September daphnid C/P > 700%. Bosminid C/P consistently > 50%	Fig 18, Table 29
Woss	2002	Bosminid C/P > 500%. Daphnid C/P about 150%.	Bosminid and daphnid C/P < 100%.	Fig 18, Table 31
Woss	2003	Bosminid C/P low (3-50%)	Mid-summer and fall daphnid C/P 1000-4000%. Daphnids almost eliminated. Bosminid C/P low (3-50%)	Fig 18, Table 33
Vernon	2000	C/P seldom > 50%	C/P seldom > 50%	Fig. 19, Table 28
Vernon	2001	C/P very low.	Some copepod diapause likely. Bosminid C/P near 200%.	Fig. 19, Table 30
Vernon	2002	Bosminid C/P near 5000%. *H. kenai* near C/P 150%.	Bosminid and *Epischura* C/P < 10%. Daphnid C/P 200-300%	Fig. 19, Table 32
Vernon	2003	All C/P low.	All C/P low.	Fig. 19, Table 34

Table 36. Calculation of the proportion of fertilizer incorporated into 0+ sockeye. P = total phosphorus. FP = fertilizer phosphorus. See text for explanation

	Woss Lake	Units	2000	2001	2002	2003
1	P loading	g ha^{-1} y^{-1}	436	534	714	541
2	Percent edible algae	%	5	14	45	12
3	FP incorporated into edible algae per 139 d	g ha^{-1}	23.9	72.7	319.9	64.1
4	Assume 15% ecological efficiency algae to fish	%	15	15	15	15
5	FP incorporated into zooplankton per 139 d	g ha^{-1}	3.6	10.9	48.0	9.6
6	Percent edible zooplankton	%	86	86	72	93
7	FP incorporated into edible zooplankton per 139 d	g ha^{-1}	3.1	9.3	34.4	9.0
8	Edible zoop production per 139 d ww	kg ha^{-1}	90	107	168	107
9	Total P into edible zooplankton production per 139 d	g ha^{-1}	96	115	181	115
10	Biomass edible zooplankton (ww) consumed by sockeye per 139 d	kg ha^{-1}	13.7	8.3	15.4	14.0

Table 36 (cont'd)

	Woss Lake	Units	2000	2001	2002	2003
11	Total P consumed by sockeye per 139 d	g h^{-1}	14.6	8.9	16.5	15.1
12	FP consumed by sockeye per 139 d	g h^{-1}	0.47	0.73	3.14	1.18
13	Mean 0+ sockeye density	ha^{-1}	650	400	624	909
14	Mean interval weight gain	g ww	2.4	2.6	2.5	2.1
15	0+ sockeye production per 139 d	g ha^{-1} ww	1589	1022	1538	1923
16	Total P incorporated by sockeye over 139 d	g ha^{-1}	5.6	3.6	5.4	6.7
17	FP incorporated into fish over 139 d	g ha^{-1}	0.18	0.29	1.02	0.53
18	Percent of incorporated fish P that is FP	%	**3.18**	**8.15**	**18.99**	**7.83**

Table 37. Percentage of Woss Lake fertilizer phosphorus = FP incorporated into algae, zooplankton and fish during year 2000-03.

	2000	2001	2002	2003
% of FP incorporated into algae	5.50	13.60	44.80	11.80
% FP incorporated into edible zooplankton	0.70	1.75	4.82	1.66
% of FP incorporated in fish	0.04	0.06	0.14	0.10

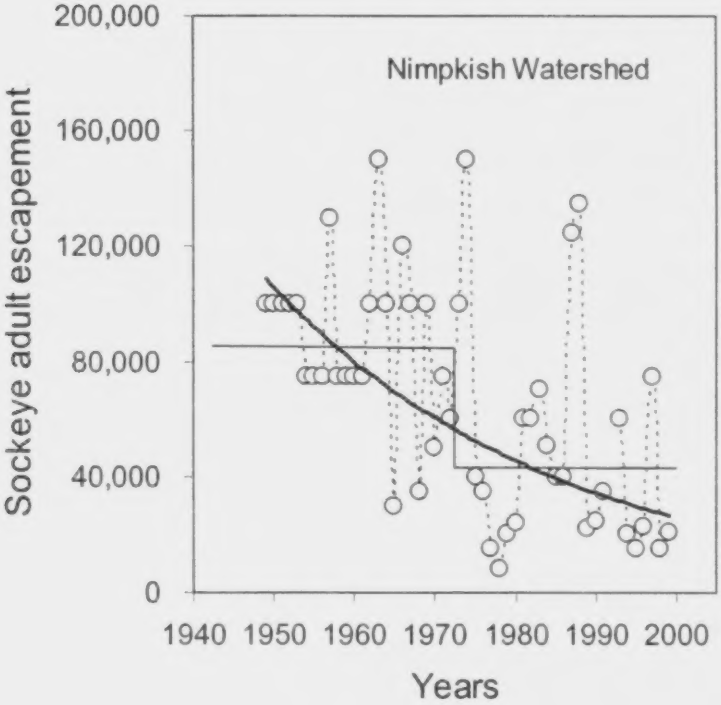


Figure 1. Mean annual sockeye escapement estimates into the Nimpkish River system.

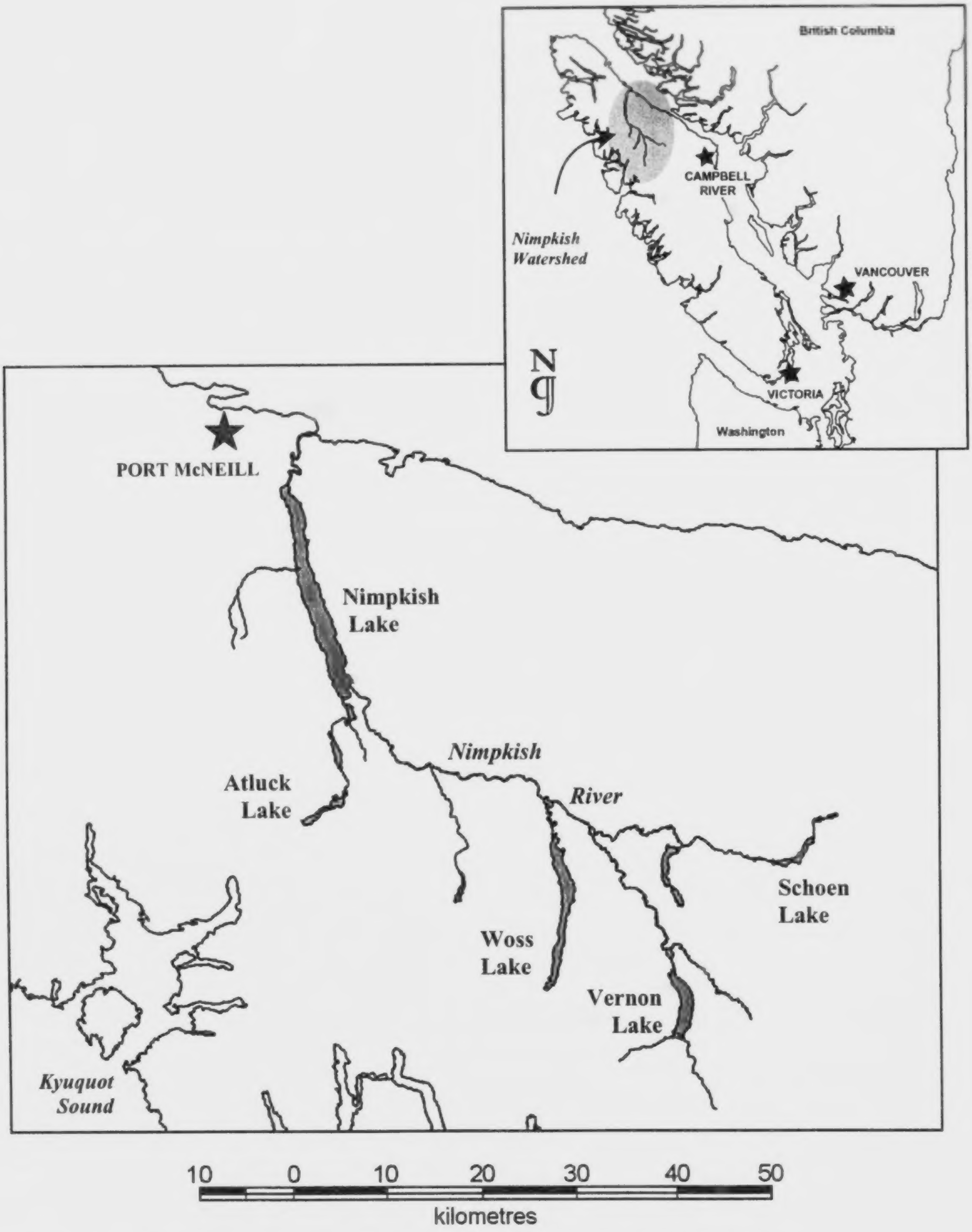

British Columbia
CAMPBELL RIVER
Nimpkish Watershed
VANCOUVER
N
VICTORIA
Washington
PORT McNEILL
Nimpkish Lake
Atluck Lake
Nimpkish River
Schoen Lake
Woss Lake
Vernon Lake
Kyuquot Sound
10 0 10 20 30 40 50
kilometres

Figure 2. Location of Woss and Vernon Lakes, North-Central Vancouver Island.

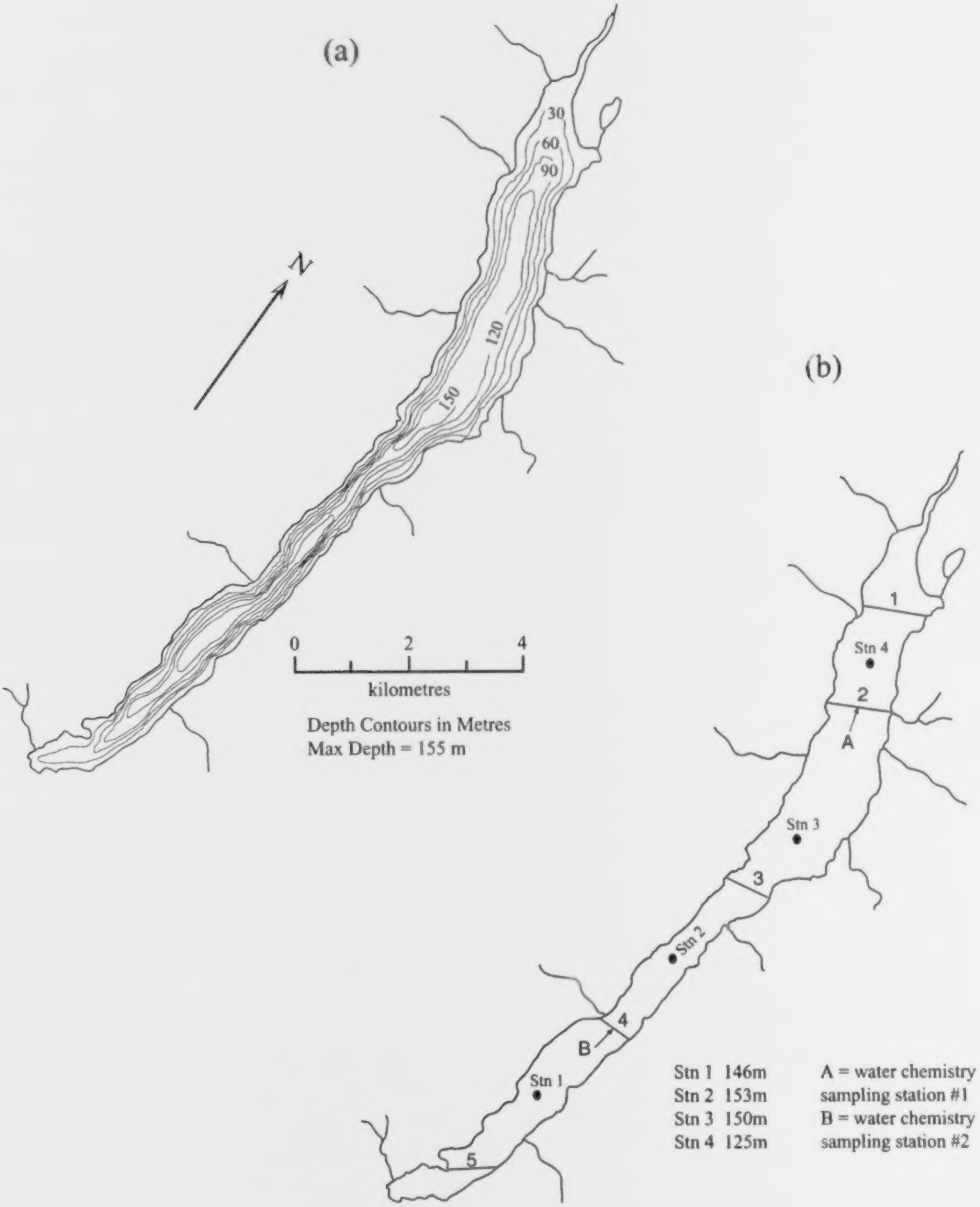

(a)
N
30
60
90
120
150
0
2
4
kilometres
Depth Contours in Metres
Max Depth = 155 m
(b)
1
Stn 4
2
A
Stn 3
3
Stn 2
4
B
Stn 1
5
Stn 1 146m
Stn 2 153m
Stn 3 150m
Stn 4 125m
A = water chemistry sampling station #1
B = water chemistry sampling station #2

Figure 3A. Figure 3A: Woss Lake (1366 ha) and Figure 3B: Vernon Lake (837 ha). Bathymetry, acoustic survey transects and sampling stations.

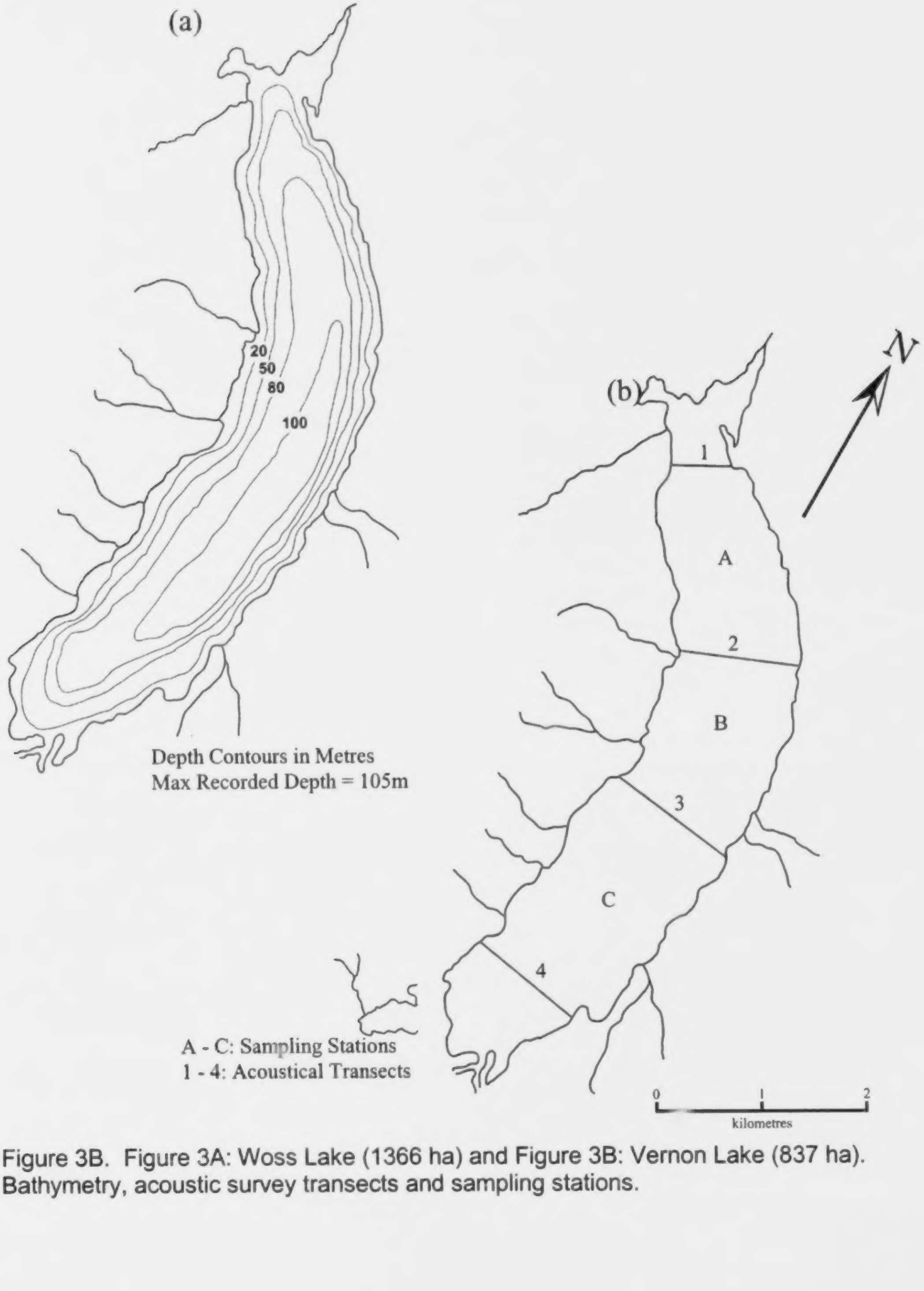

(a)
20
50
80
100
Depth Contours in Metres
Max Recorded Depth = 105m
(b)
N
1
A
2
B
3
C
4
A - C: Sampling Stations
1 - 4: Acoustical Transects
0
1
2
kilometres

Figure 3B. Figure 3A: Woss Lake (1366 ha) and Figure 3B: Vernon Lake (837 ha). Bathymetry, acoustic survey transects and sampling stations.

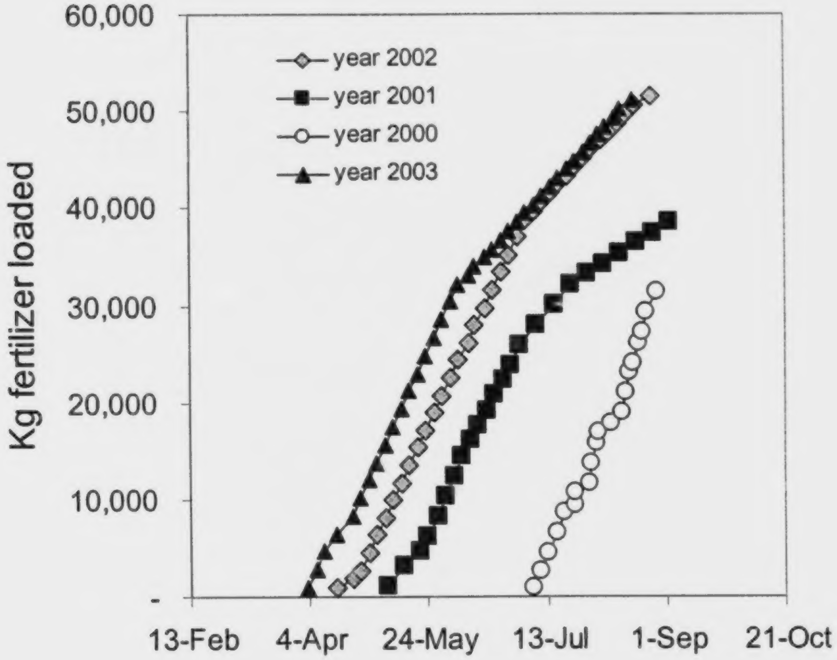


Figure 4. Cumulative total fertilizer (kg) added to Woss Lake during 2000 - 03.

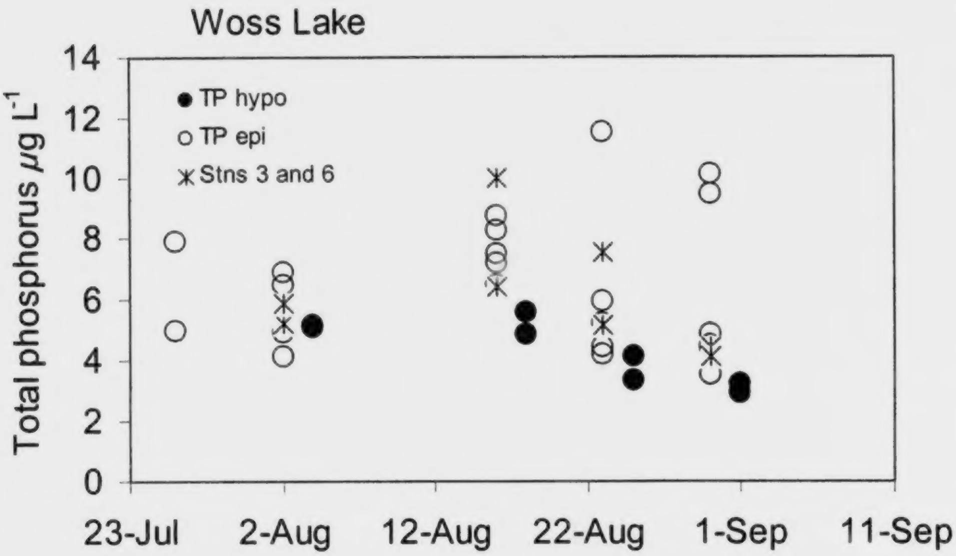


Figure 5. Total phosphorus concentrations from 3 m (epilimnion) and 25 m (hypolimnion) samples taken from Woss Lake on five dates during 2000. The star symbols represent stations on the center-line on Woss Lake.

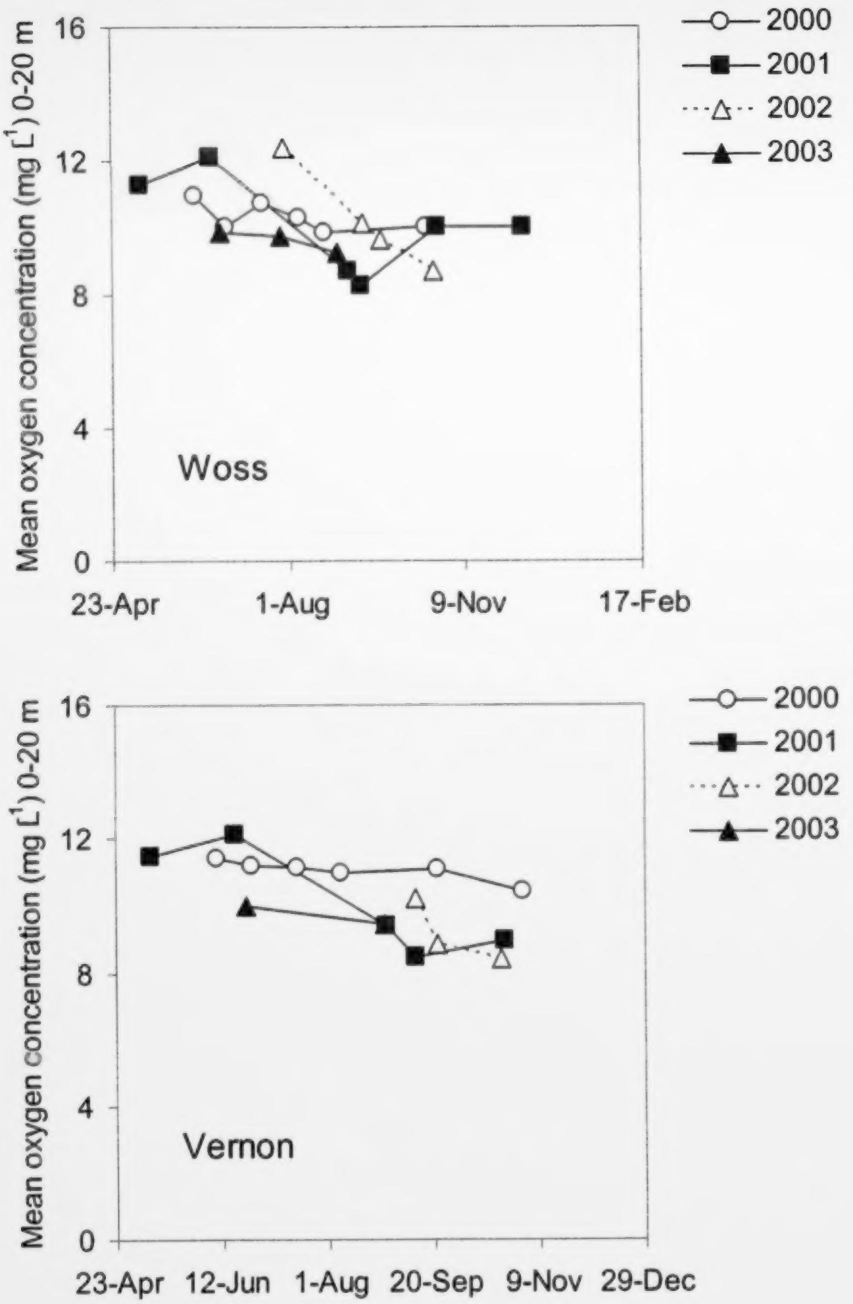
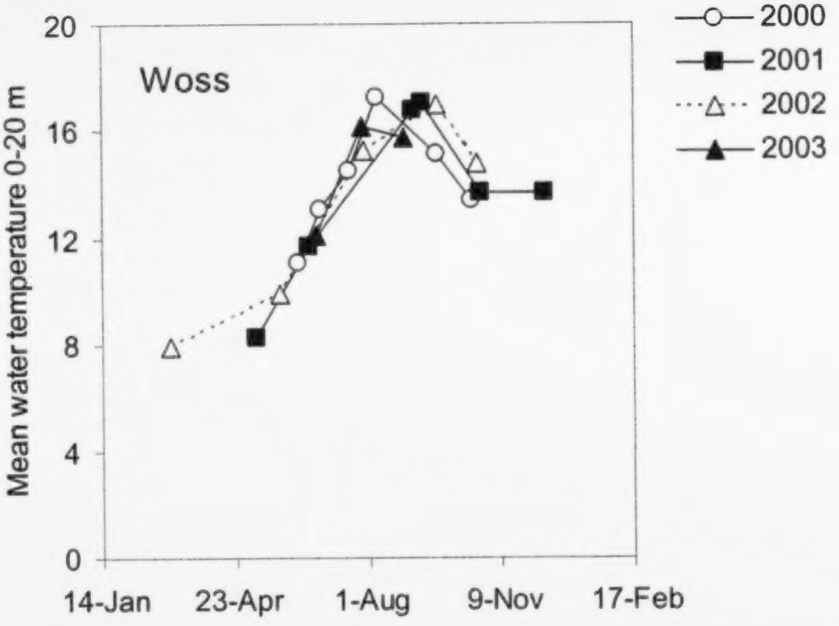


Figure 6. Mean epilimnetic (0 – 20 m) oxygen concentrations in Woss and Vernon Lakes.

Figure 7



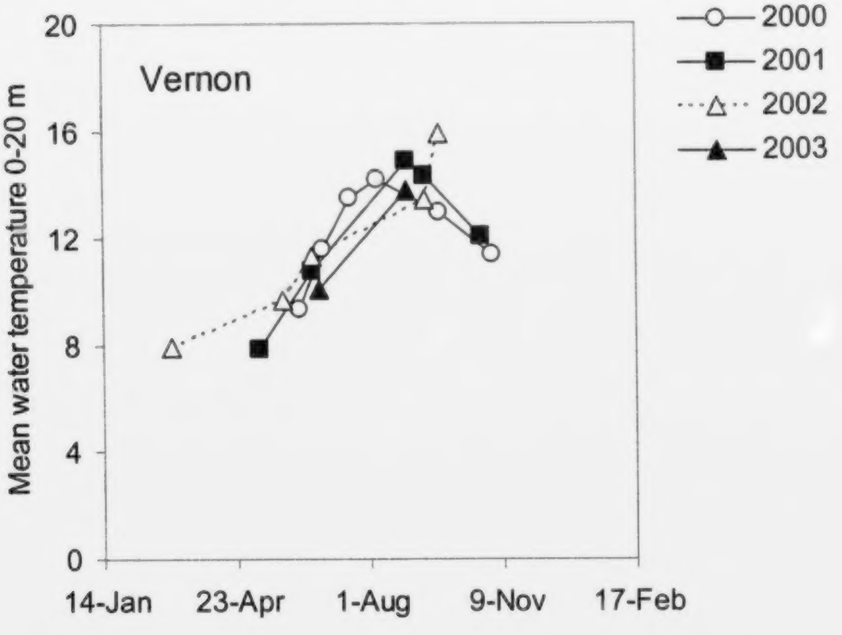


Figure 7. Mean epilimnetic (0 – 20 m) water temperatures in Woss and Vernon Lakes.

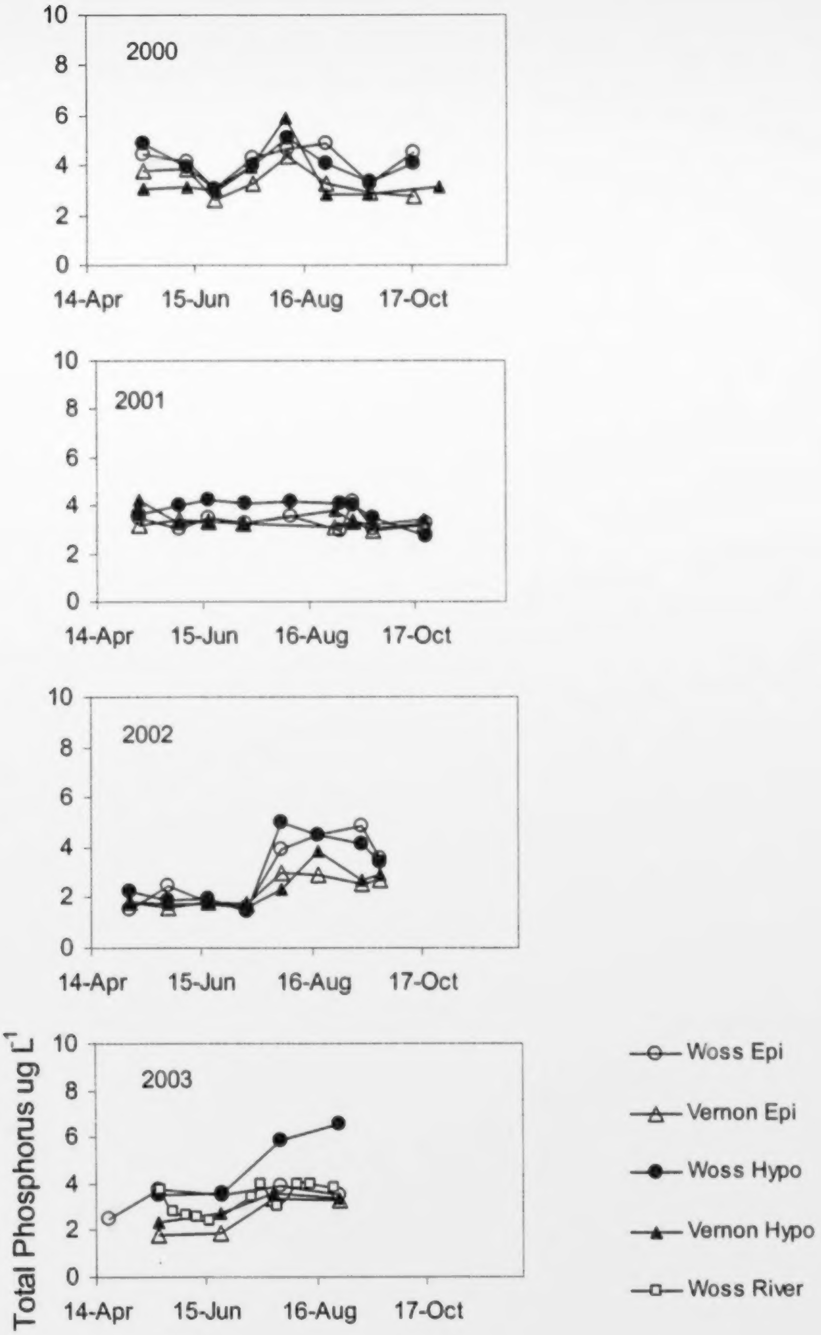


Figure 8. Total phosphorus concentrations in Woss and Vernon Lakes.

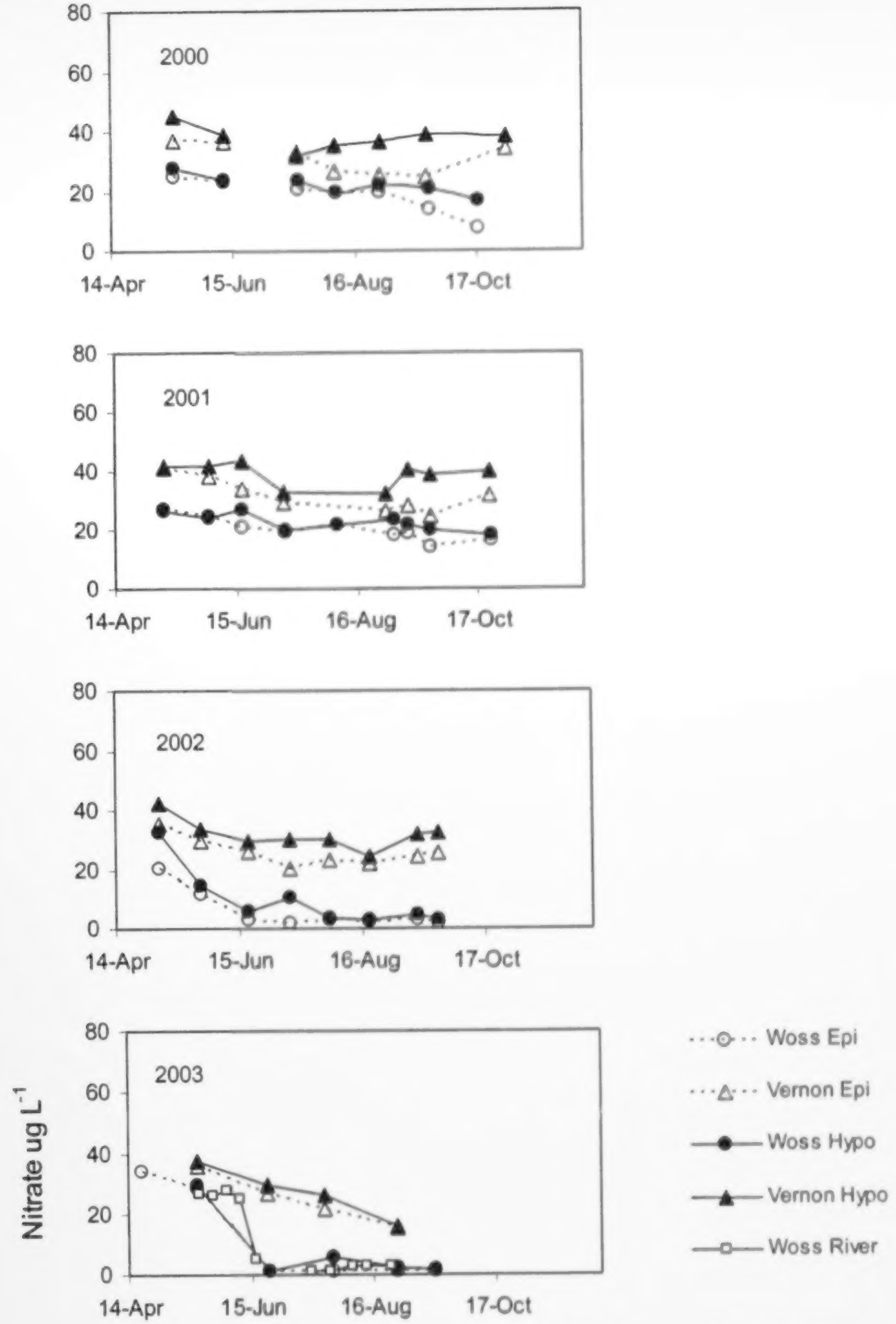


Figure 9. Nitrate plus nitrite concentrations in Woss and Vernon Lakes.

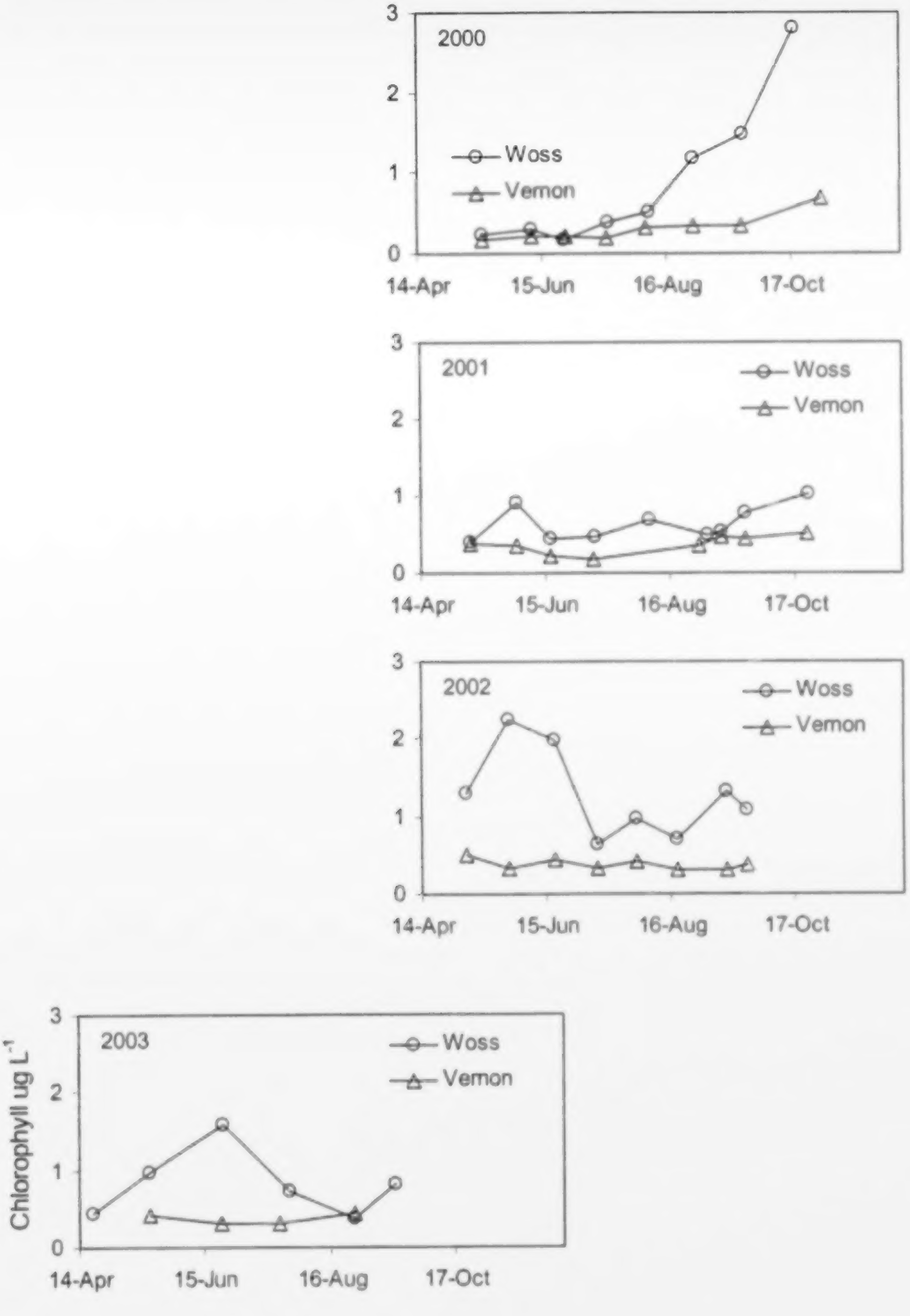


Figure 10. Chlorophyll a concentrations in Woss and Vernon Lakes.

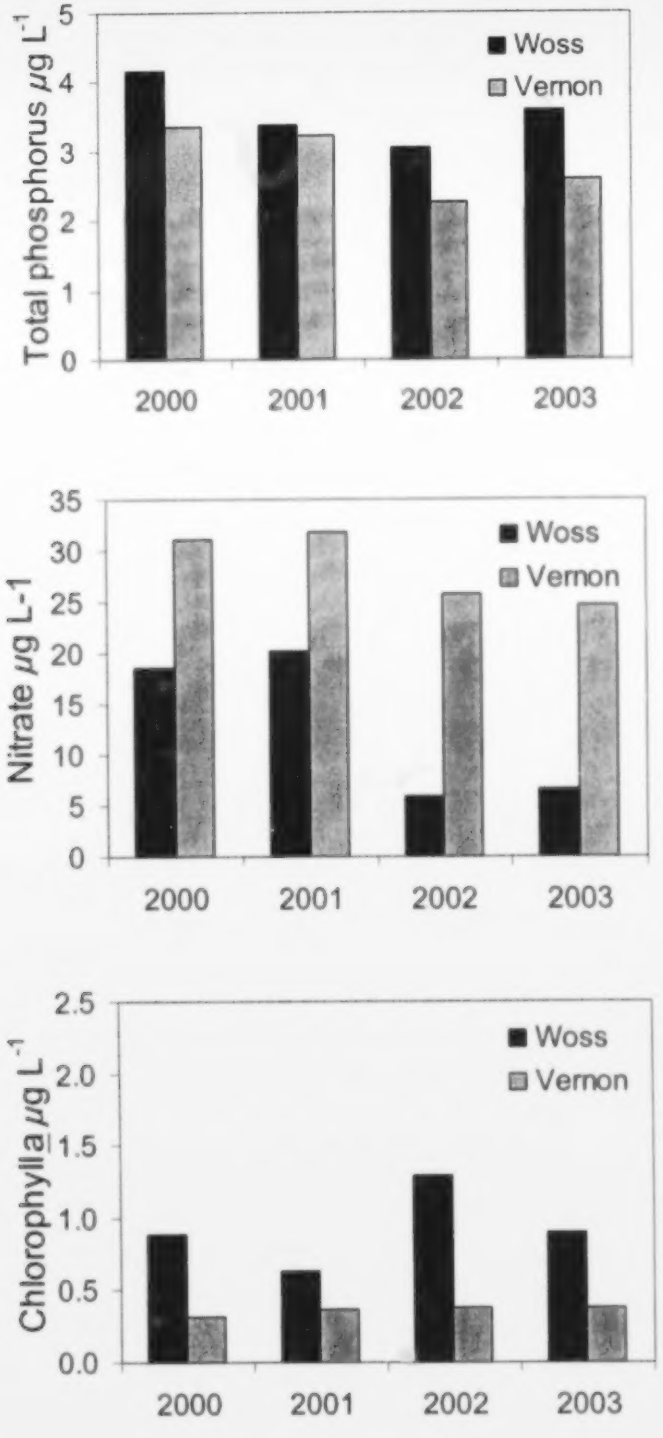


Figure 11. Mean annual (May – October) phosphorus, nitrate + nitrite, and chlorophyll a concentrations in Woss and Vernon Lakes.

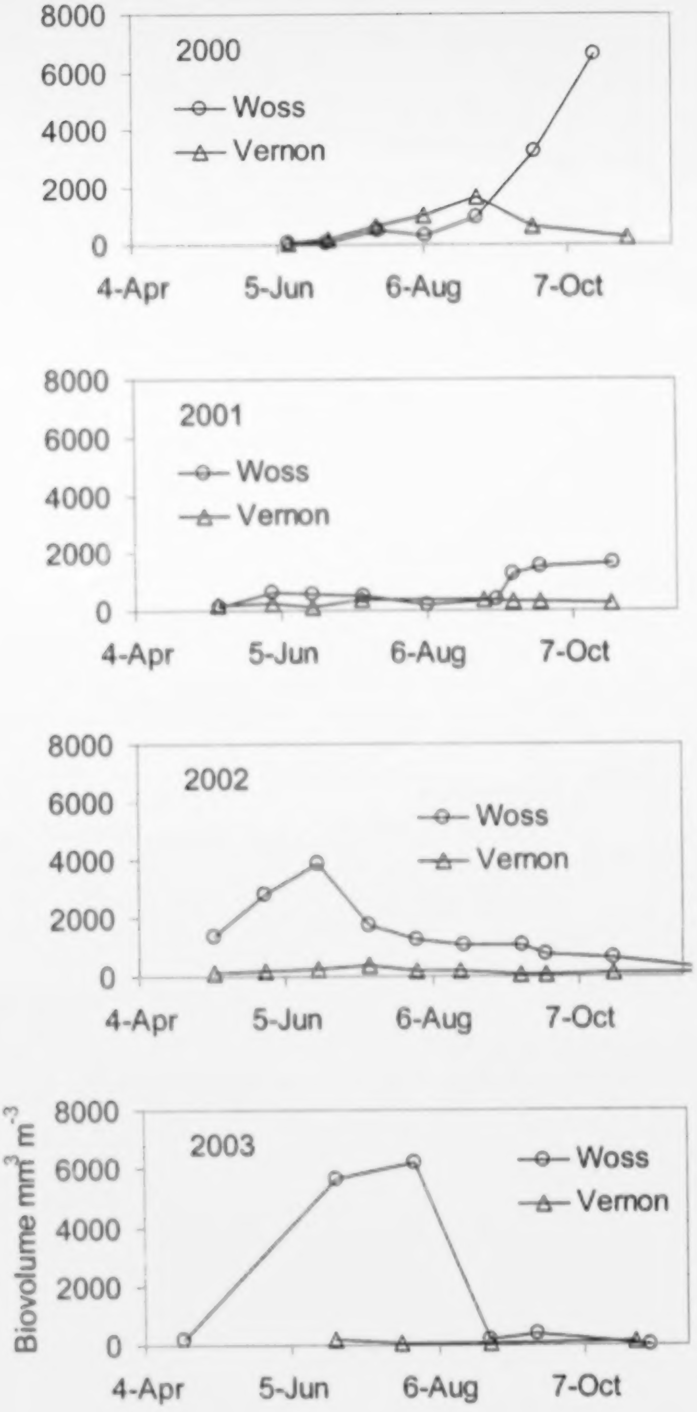


Figure 12. Total algal biovolumes in Woss and Vernon Lakes.

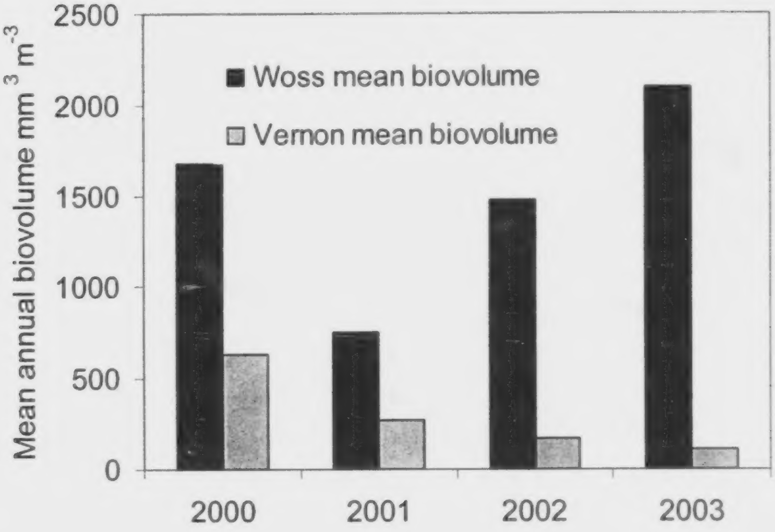


Figure 13. Mean annual algal biovolumes (May - October) in Woss and Vernon Lakes.

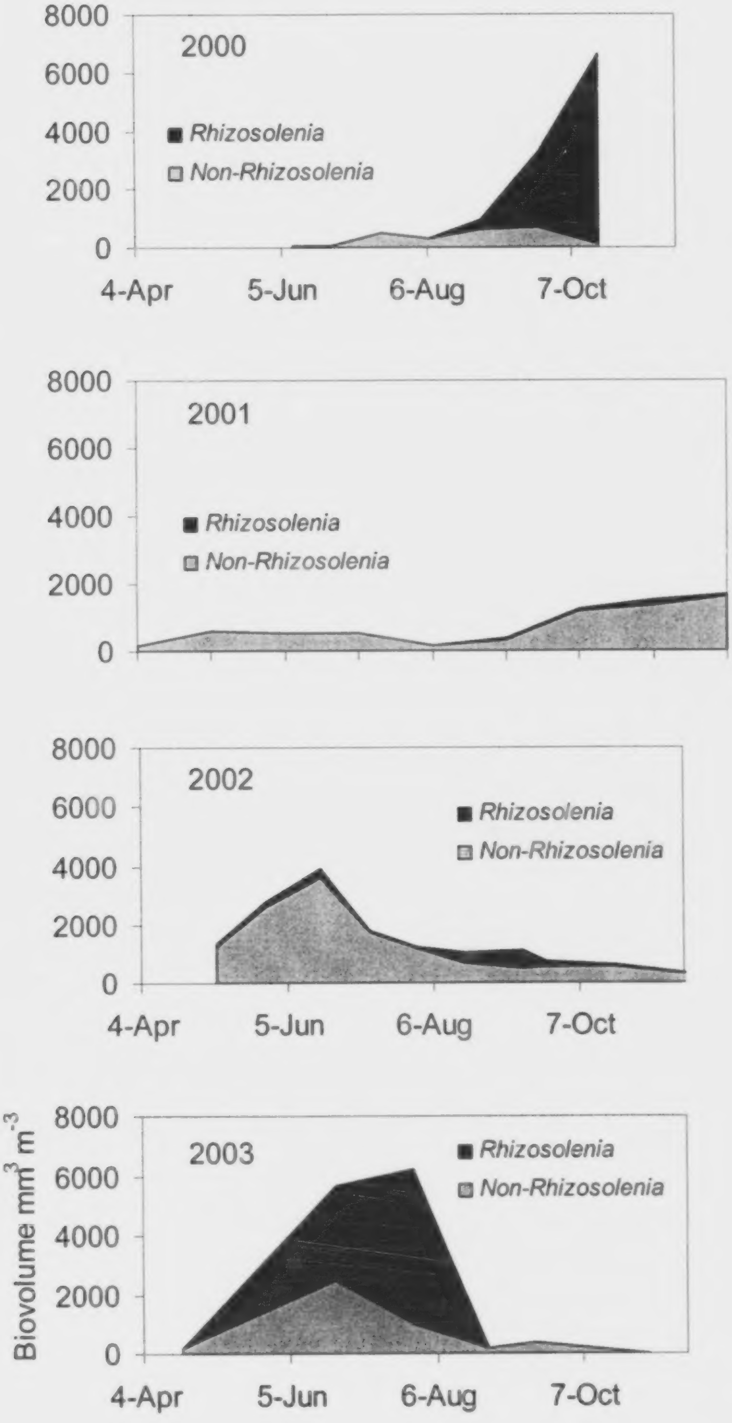


Figure 14. Woss Lake total algal biovolumes divided into *Rhizosolenia* biovolumes and summed biovolumes of all remaining algal taxa.

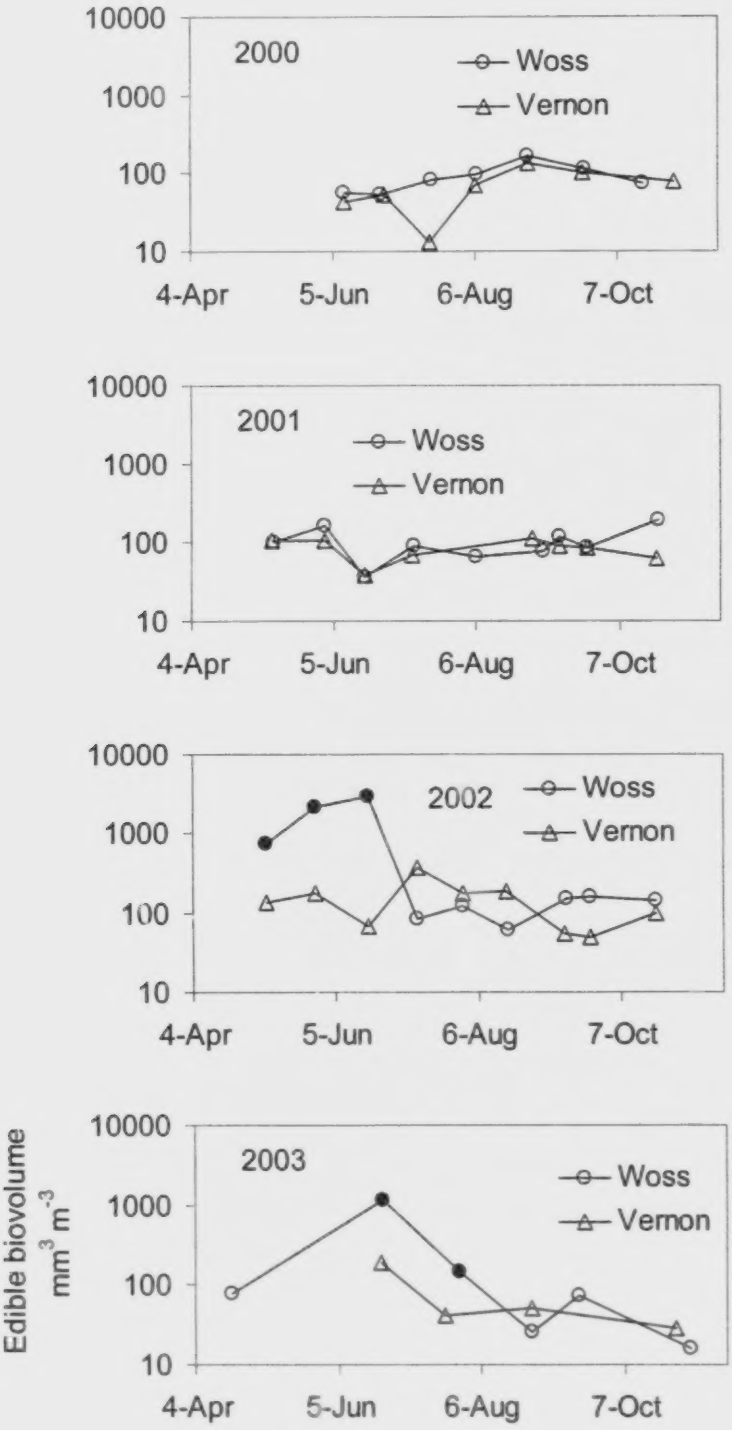


Figure 15: Edible algal biovolumes in Woss and Vernon Lakes. The dark Woss Lake symbols in the 2002 and 2003 panels represent blooms of a new and unidentified block-shaped edible diatom measuring 20 x 8 x 4 µm.

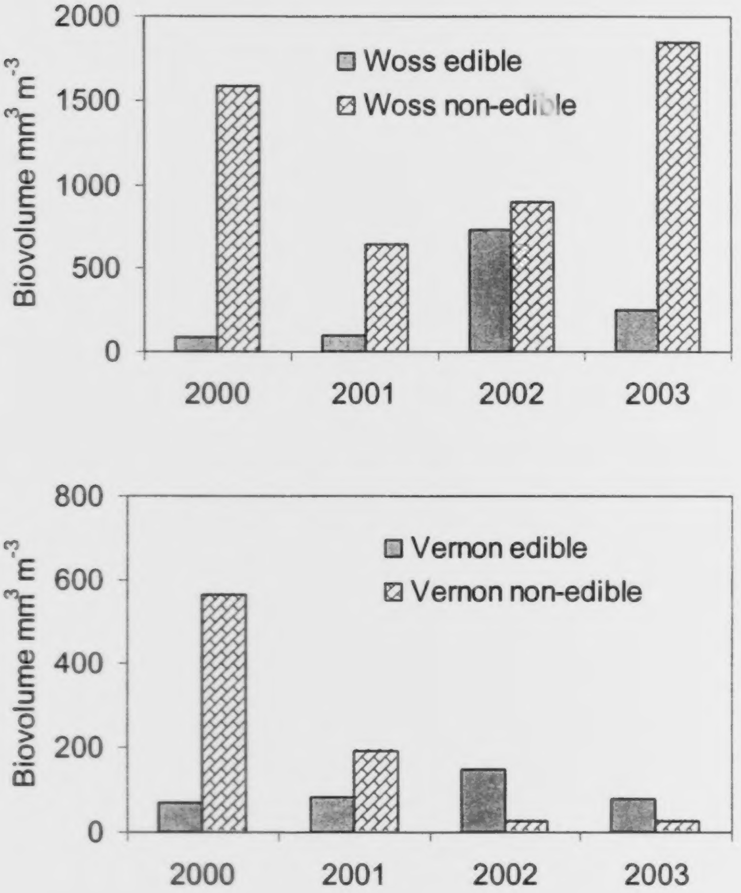


Figure 16. Edible mean annual (May - October) algal biovolumes compared to non-edible annual (May – October) algal biovolumes in Woss and Vernon Lakes.

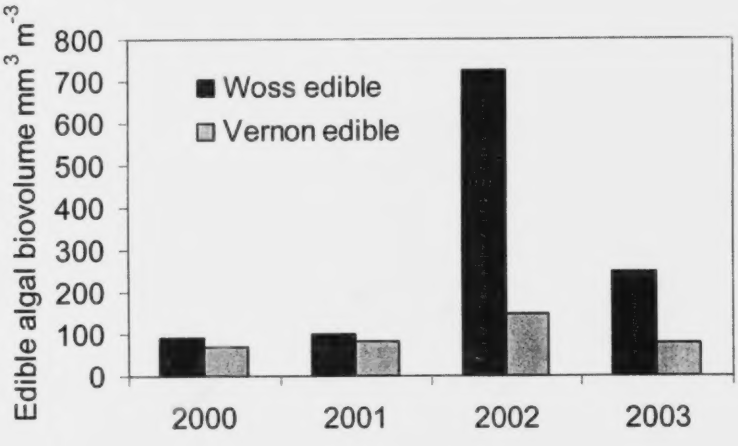


Figure 17. Edible mean annual (May - October) algal biovolumes in Woss and Vernon Lakes.

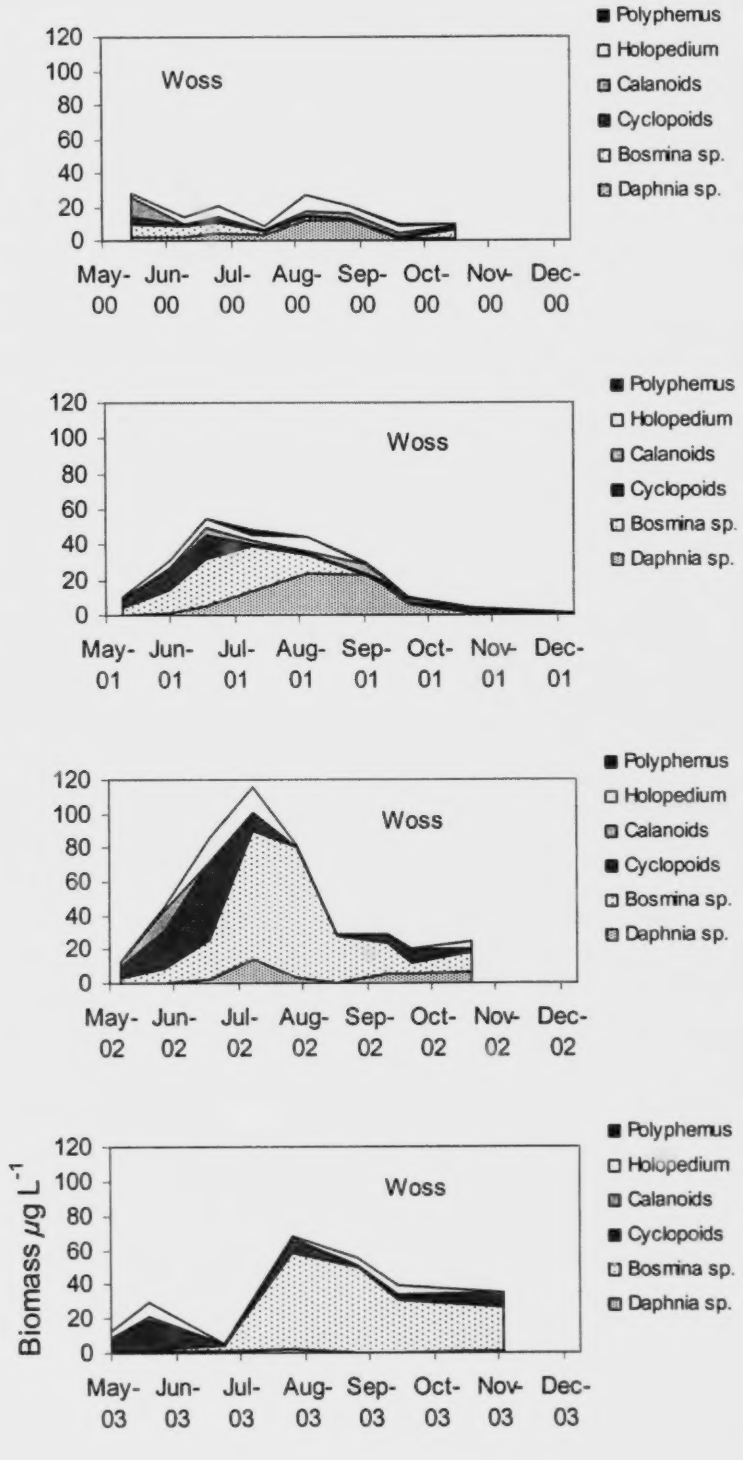


Figure 18. Woss Lake zooplankton biomasses (μg L^{-1} dry weight).

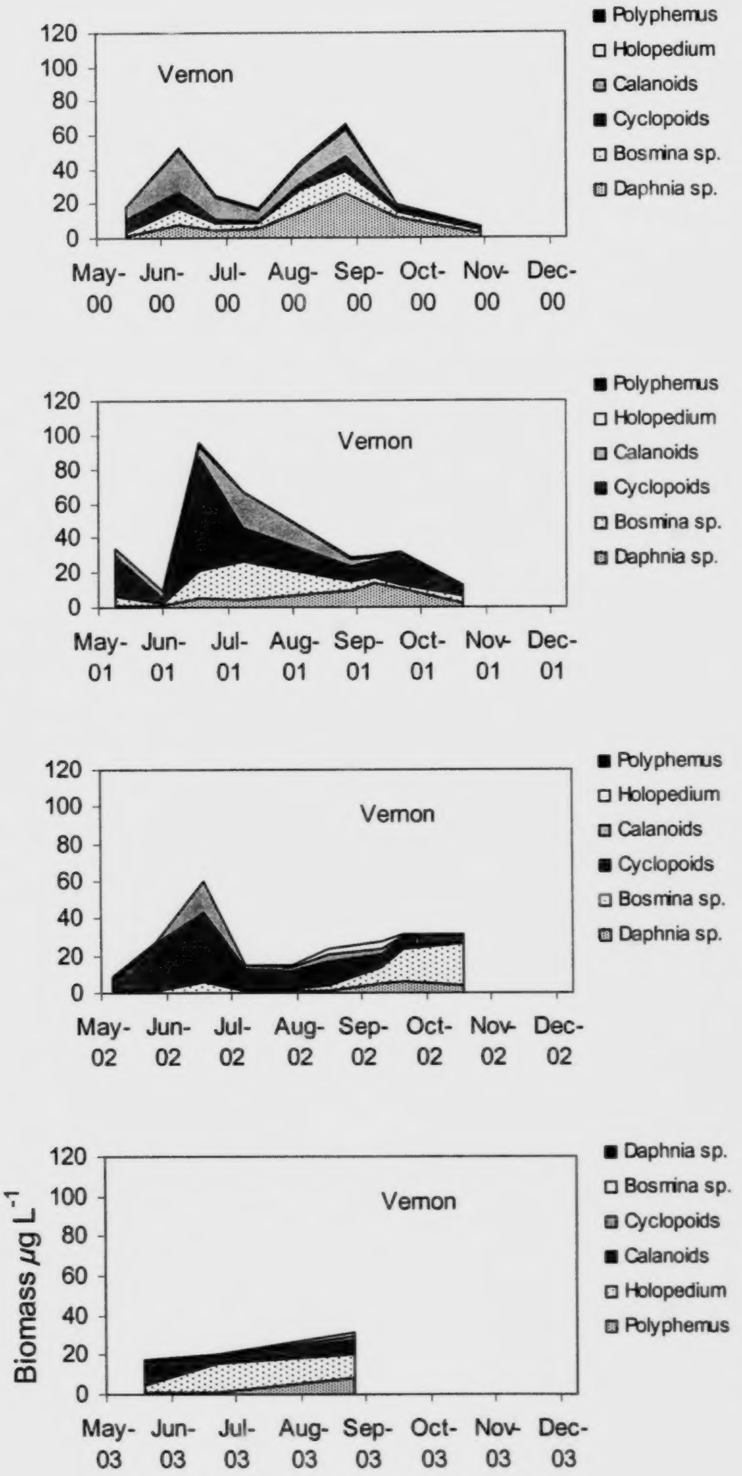


Figure 19. Vernon lake zooplankton biomasses (µg L^{-1} dry weight).

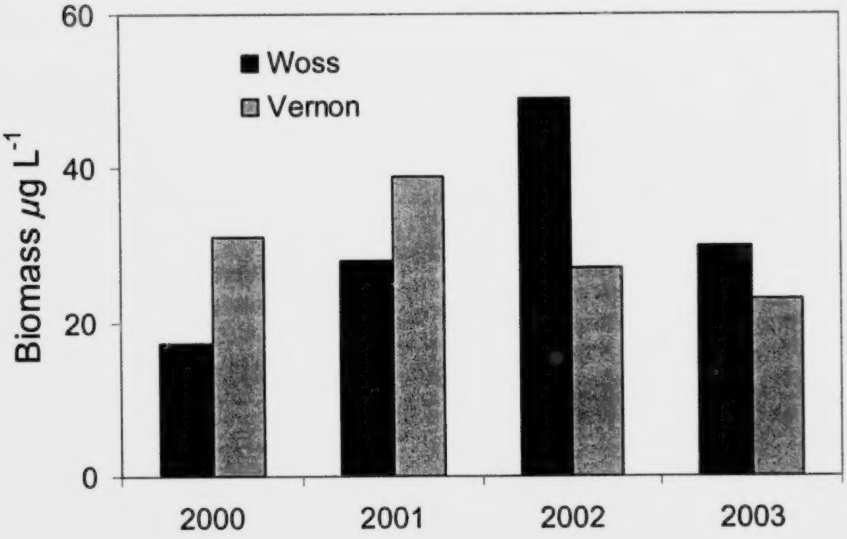


Figure 20. Mean annual Woss and Vernon Lake zooplankton biomasses (µg L^{-1} dry weight).

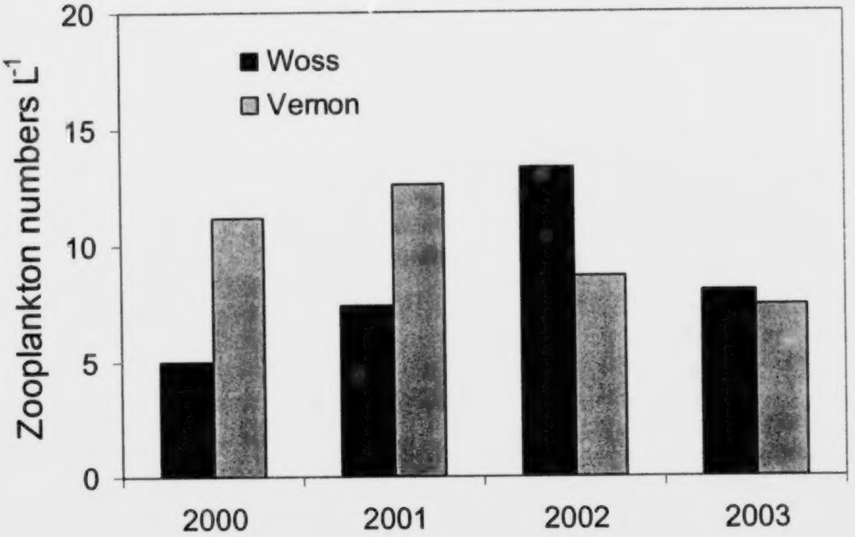


Figure 21. Mean zooplankton densities in Woss and Vernon Lakes.

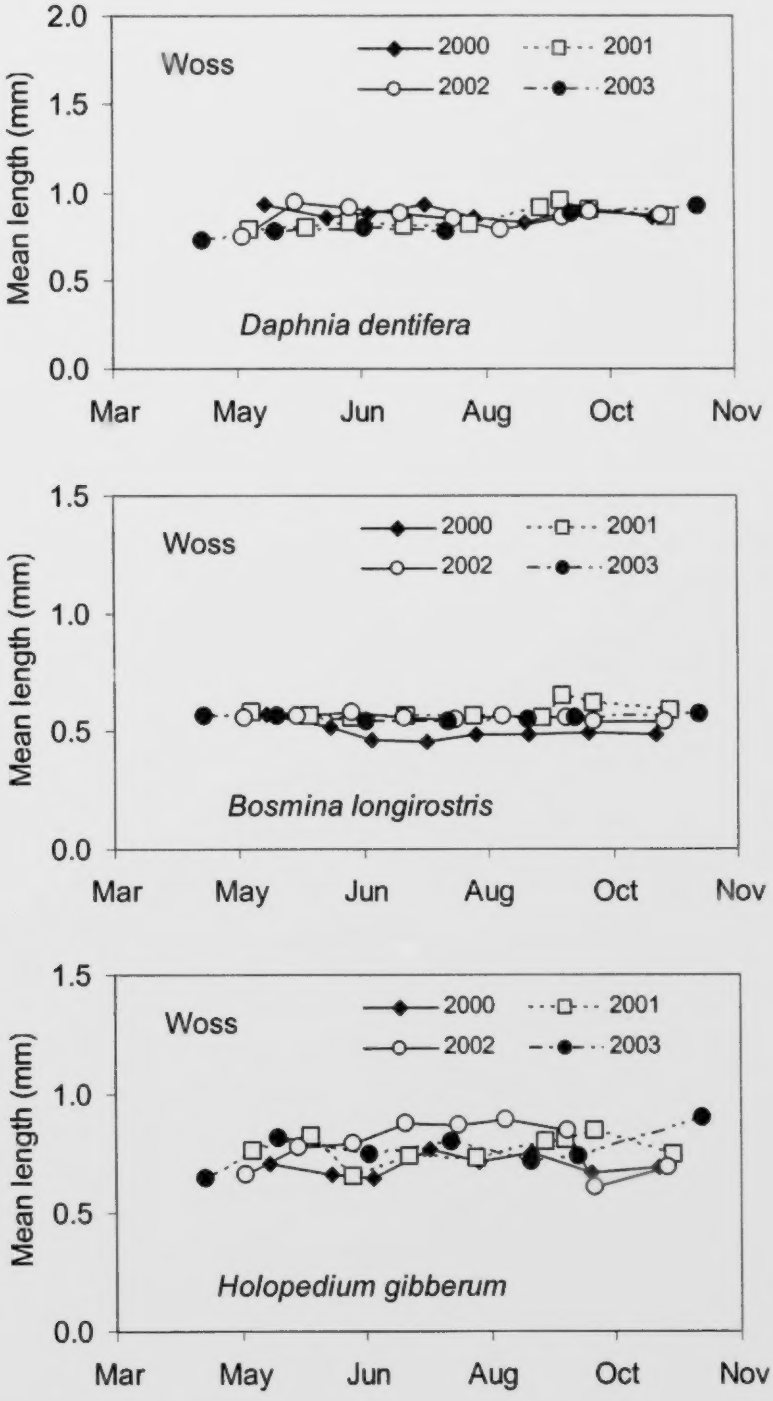


Figure 22. Woss Lake, mean lengths of abundant zooplankton species.

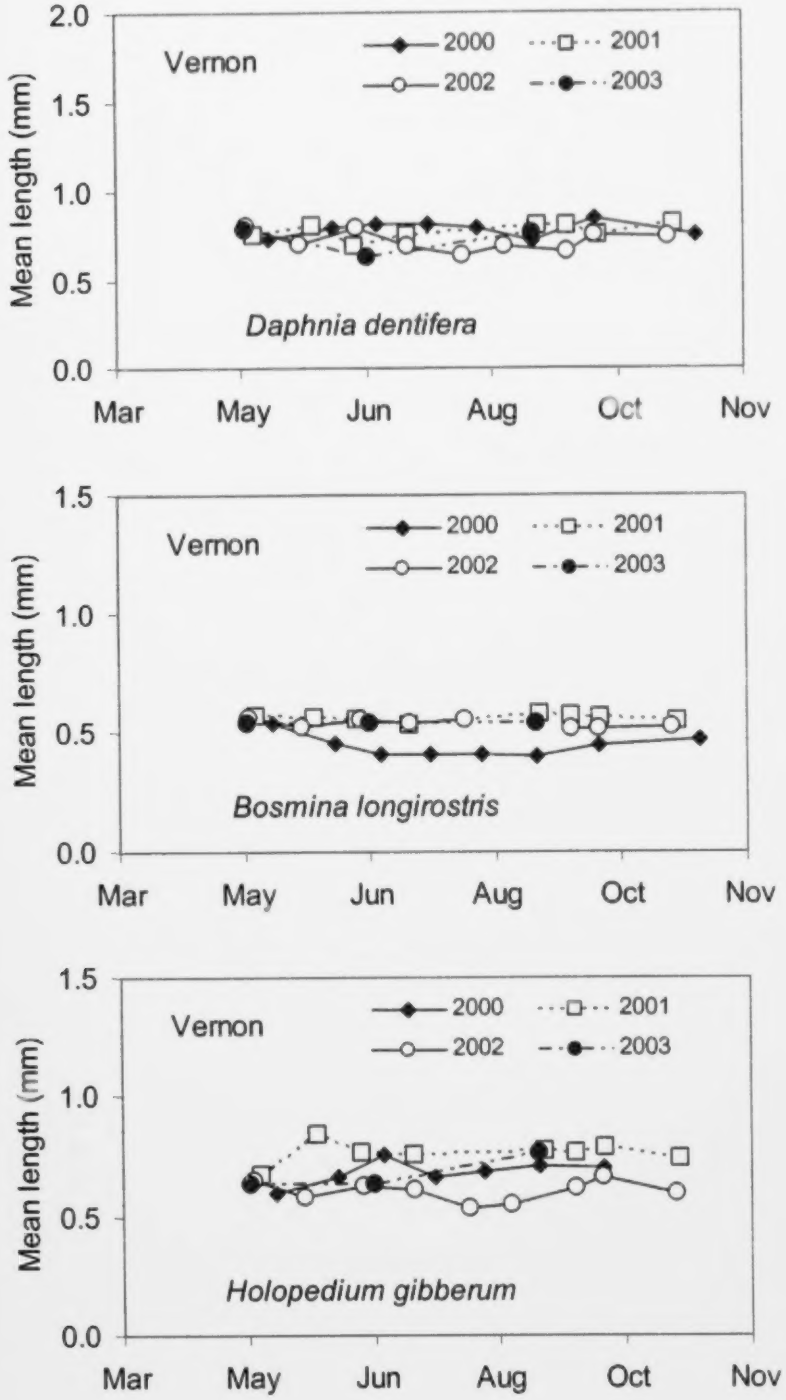
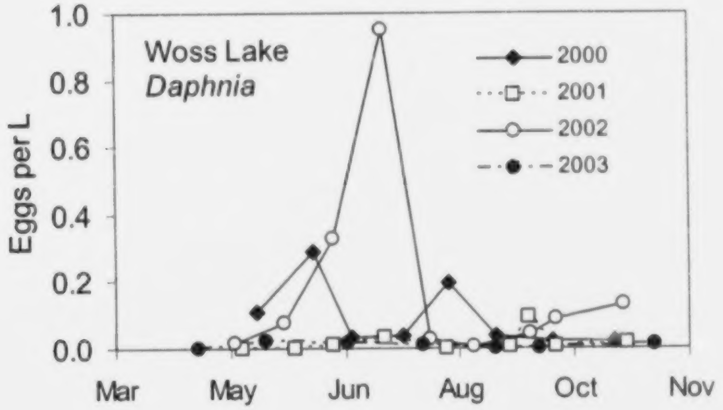
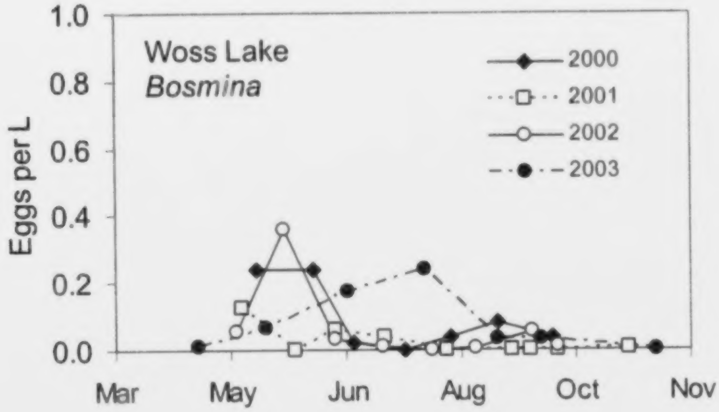


Figure 23. Vernon Lake, mean lengths of abundant zooplankton species.





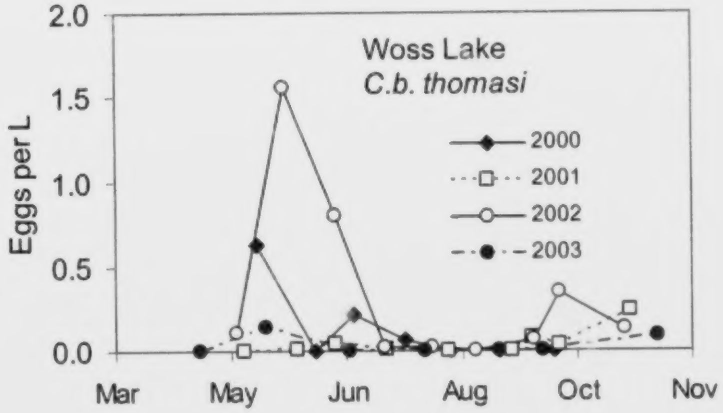


Figure 24. Woss Lake egg densities for all *Daphnia* combined, all *Bosmina* combined and for *C. b. thomasi*.

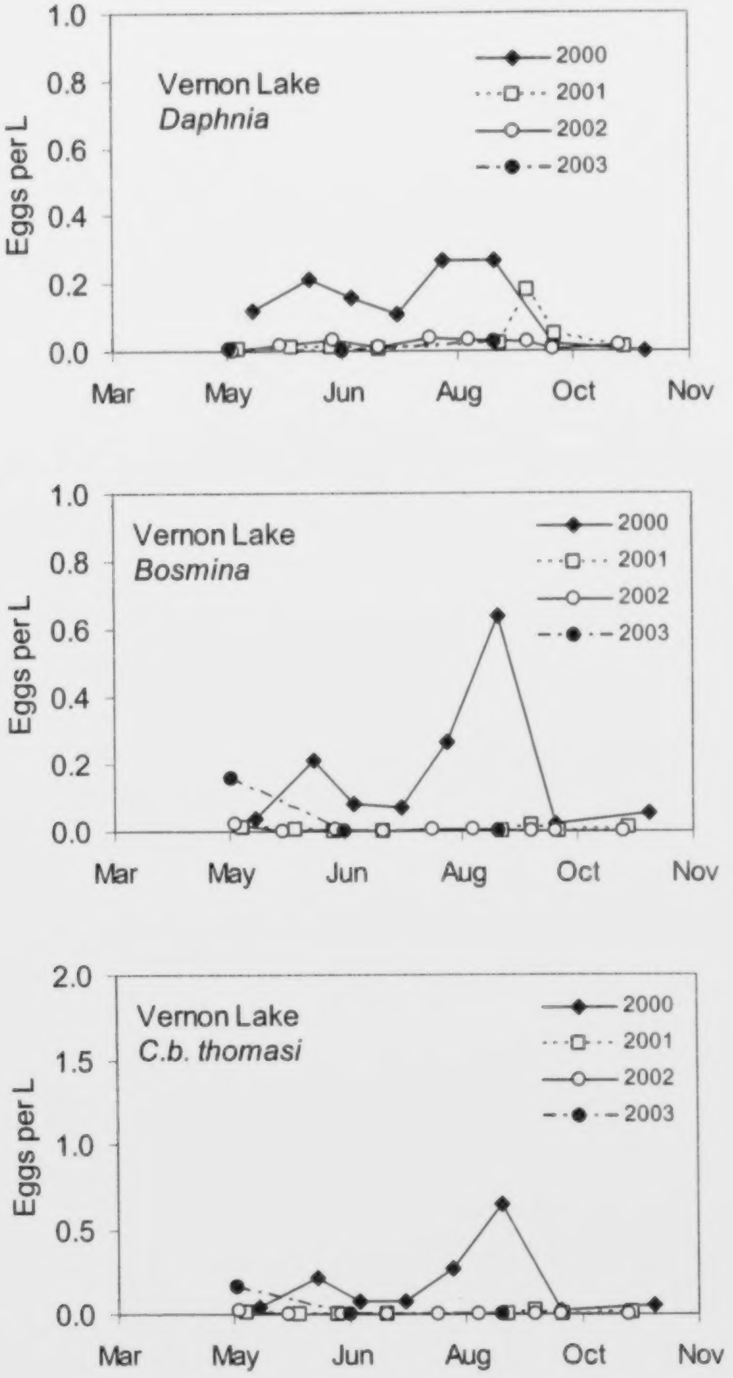


Figure 25. Vernon Lake egg densities for all *Daphnia* combined, all *Bosmina* combined and for *C. b. thomasi*.

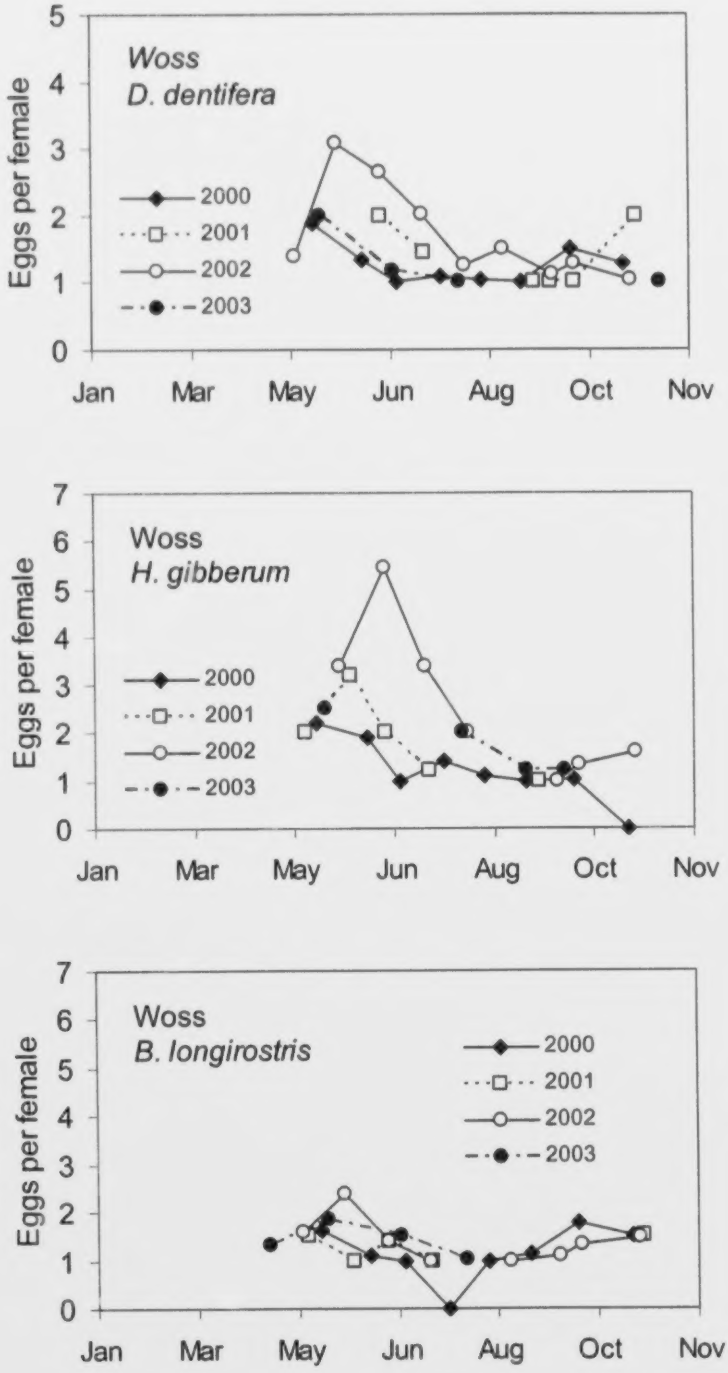


Figure 26. Woss Lake brood sizes per egg-carrying female.

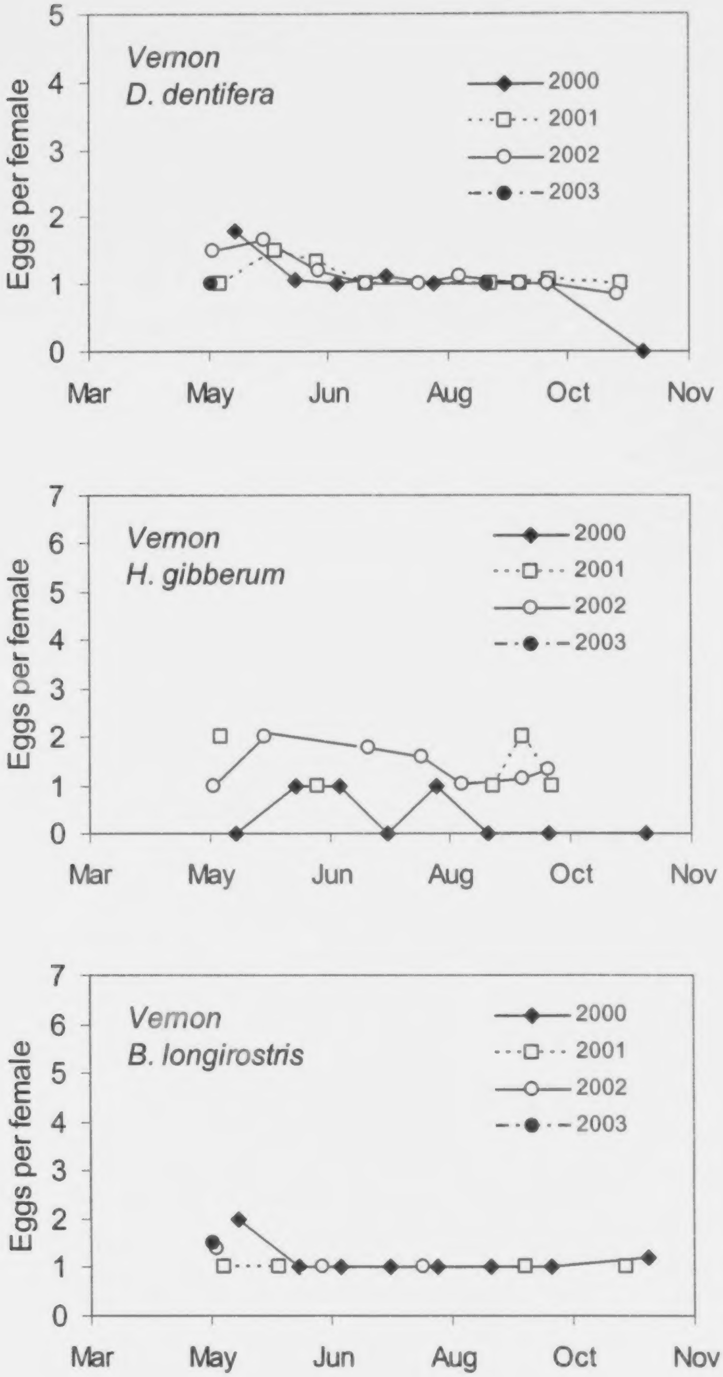


Figure 27. Vernon Lake brood sizes per egg-carrying female.

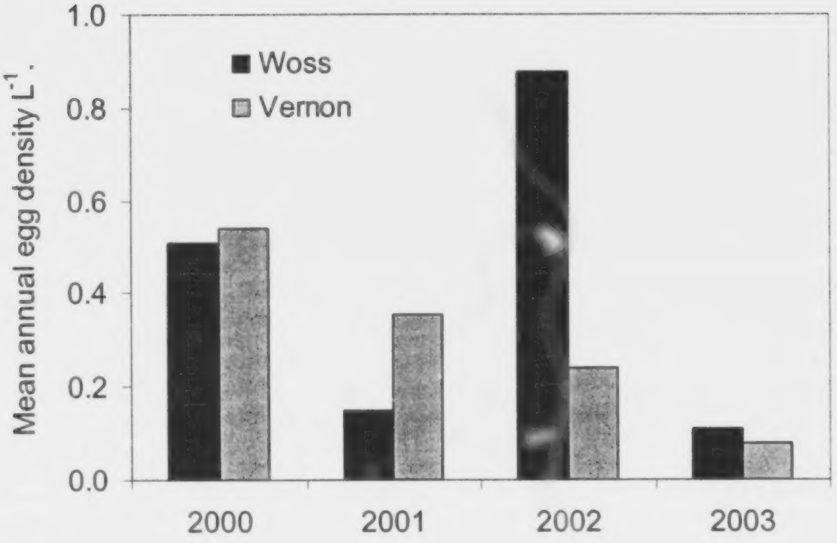


Figure 28. Mean annual (May – October) eggs numbers L^{-1} for all zooplankton combined.

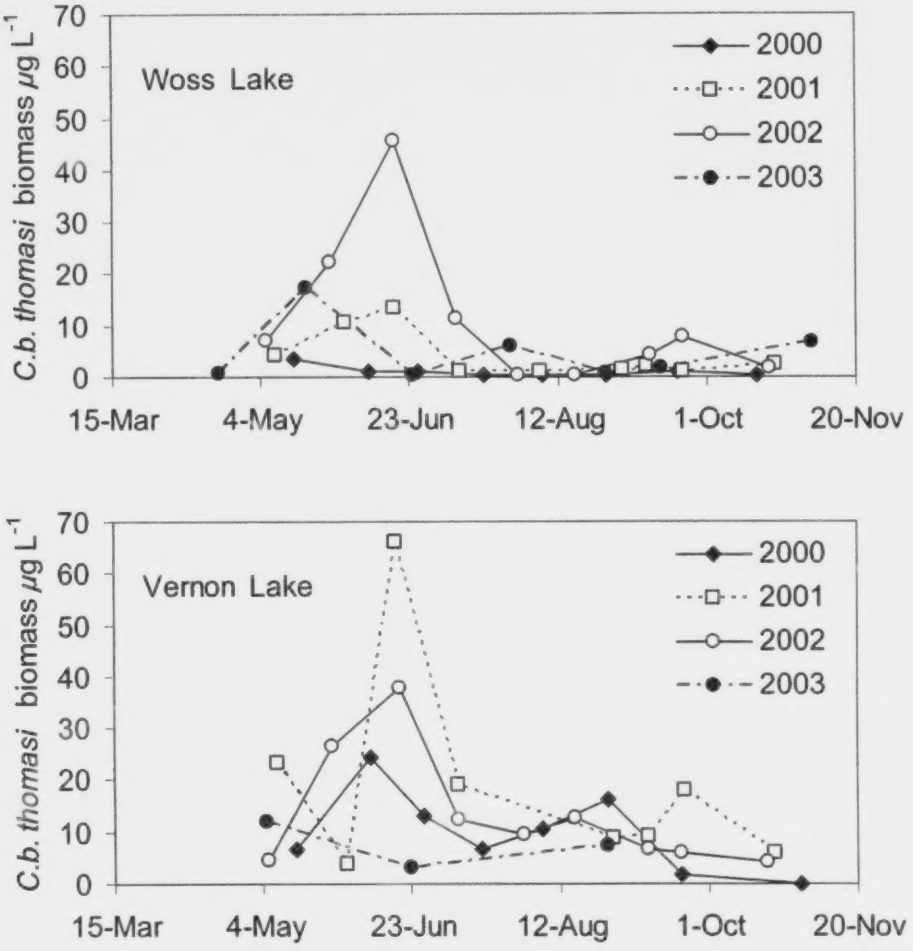


Figure 29. Biomasses of *Cyclops bicuspidatus thomasi* copepodids and adults in Woss and Vernon Lakes.

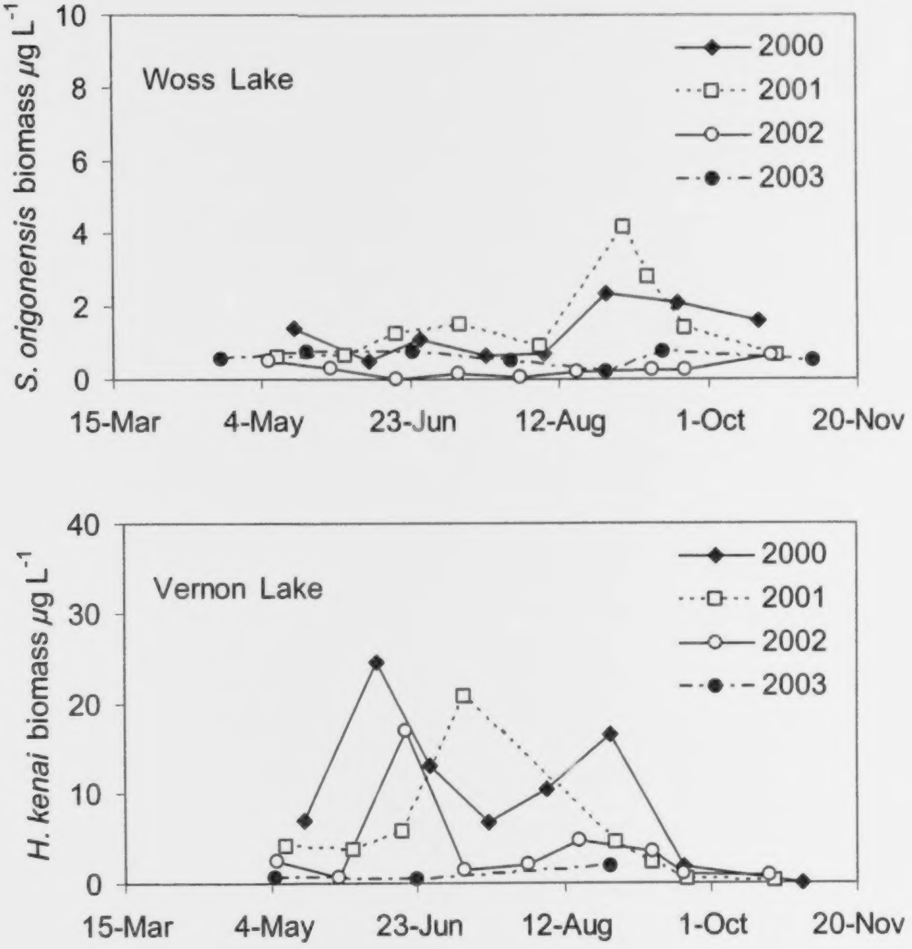


Figure 30. Biomasses of adult and copepodid *Skistodiaptomus oregonensis* in Woss Lake and *Hesperodiaptomus kenai* in Vernon Lake.

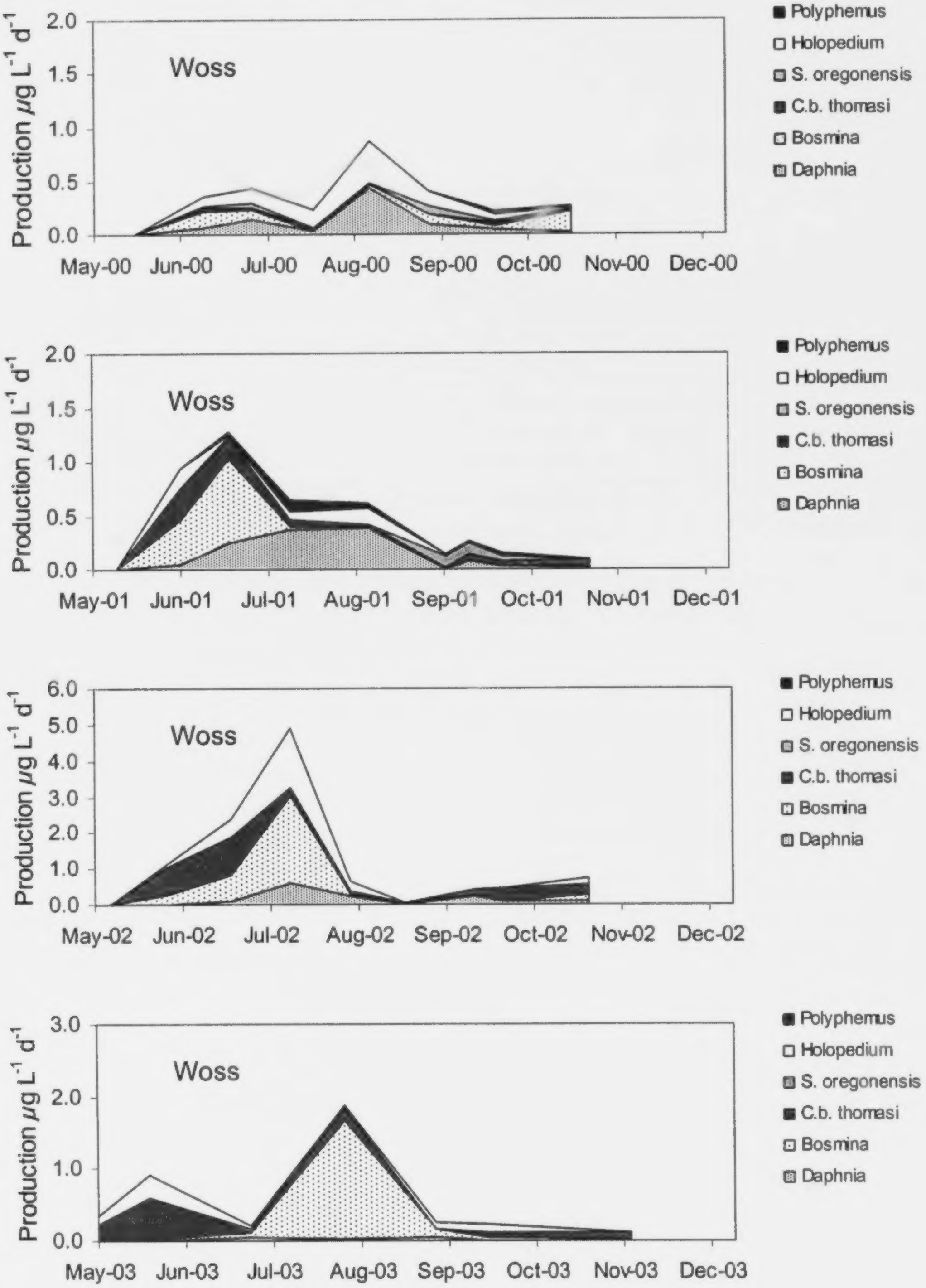


Figure 31. Zooplankton production (µg L^{-1} d^{-1} dry weight) at Woss Lake during 2000-03. Note that the scales change from panel to panel. Biomass and production for the three copepod species include data for adults plus copepodids. Nauplii have been excluded. Biomass and production for cladocerans include all growth stages.

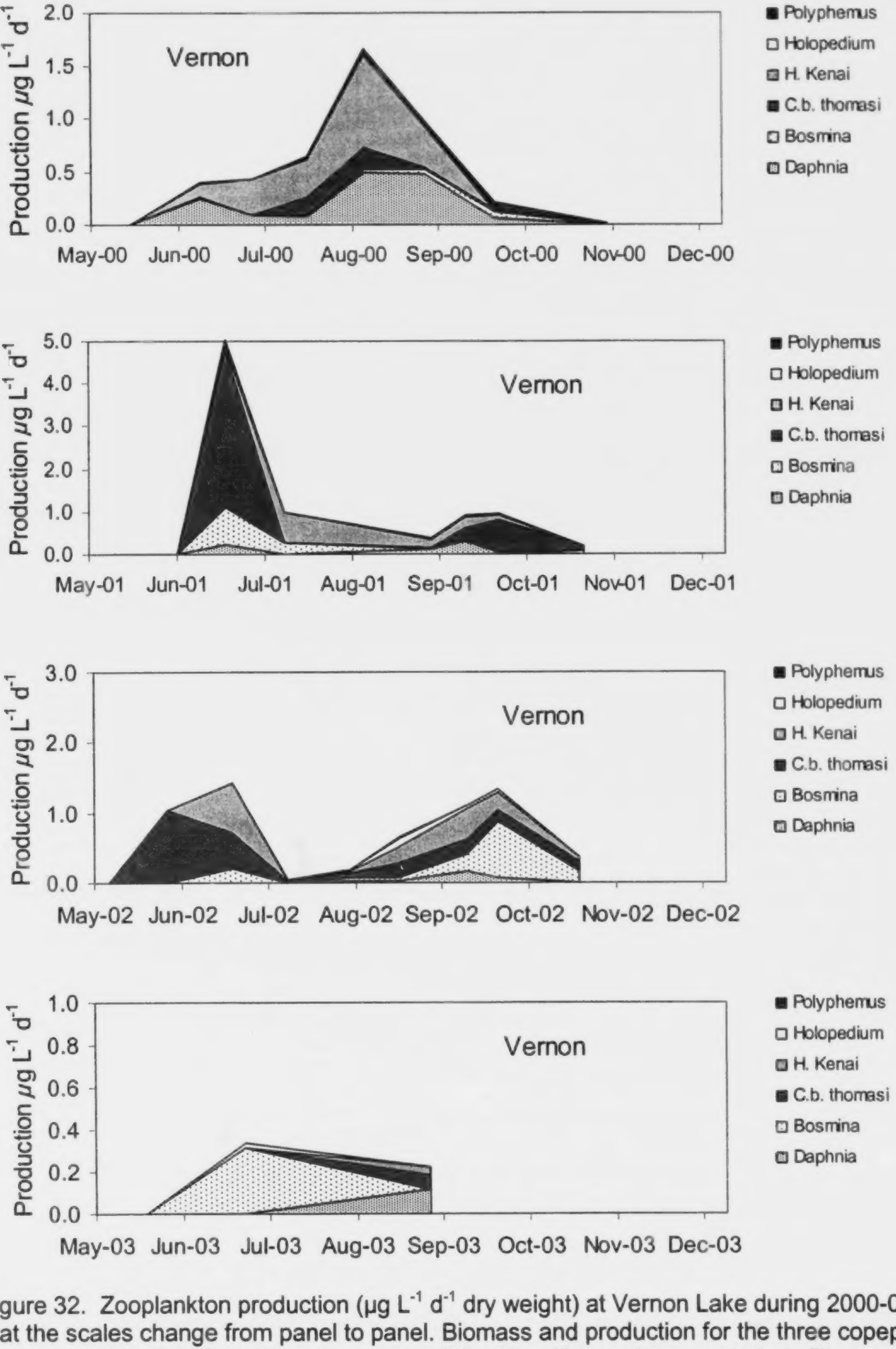
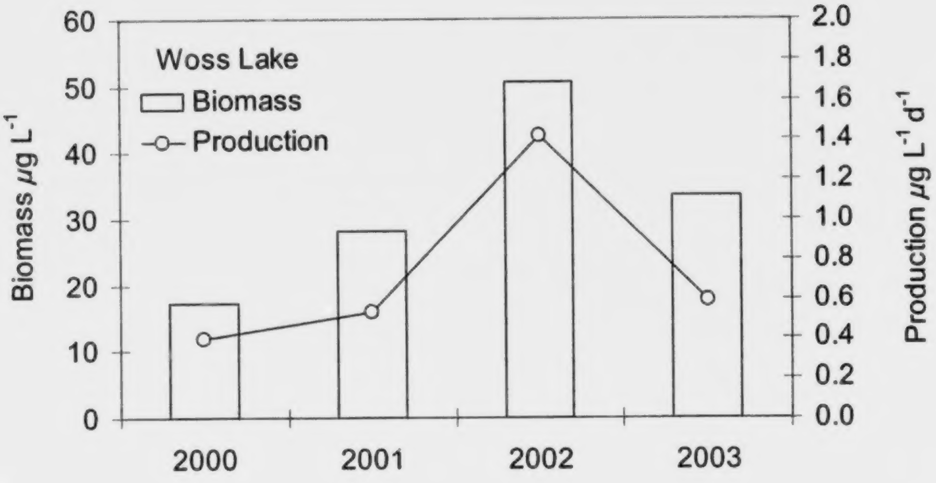


Figure 32. Zooplankton production (μg L^{-1} d^{-1} dry weight) at Vernon Lake during 2000-03. Note that the scales change from panel to panel. Biomass and production for the three copepod species include data for adults plus copepodids. Nauplii have been excluded. Biomass and production for cladocerans include all growth stages.



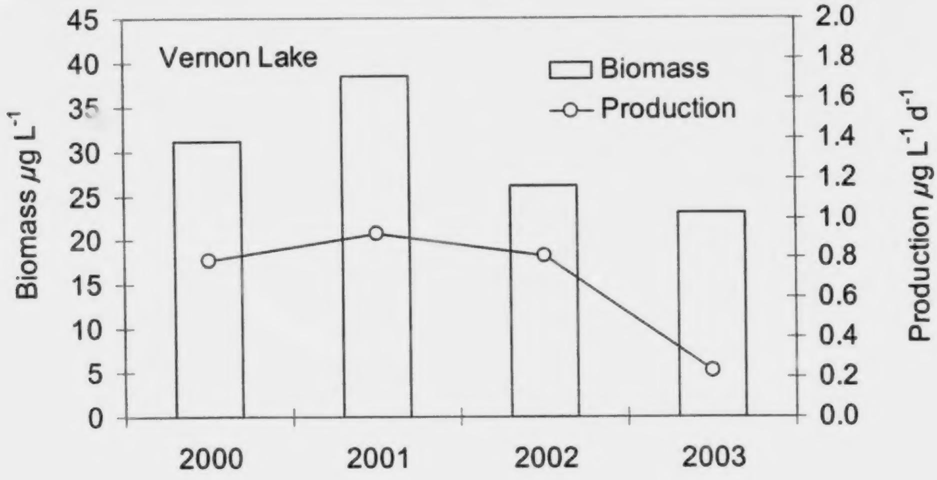


Figure 33. Mean daily growing sampling season (May-October) zooplankton biomass (µg L^{-1} dry weight) and production (µg L^{-1} d^{-1} dry weight) in Woss and Vernon Lakes. Biomass and production for the three copepod species include data for adults plus copepodids. Nauplii have been excluded. Biomass and production for cladocerans include all growth stages.

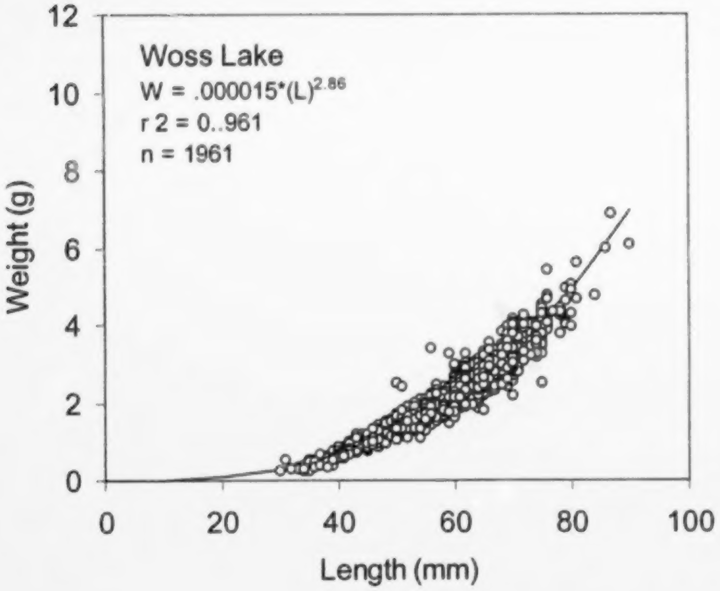


Figure 34. Woss Lake juvenile *O. nerka* length-weight regression. Includes all data from all years.

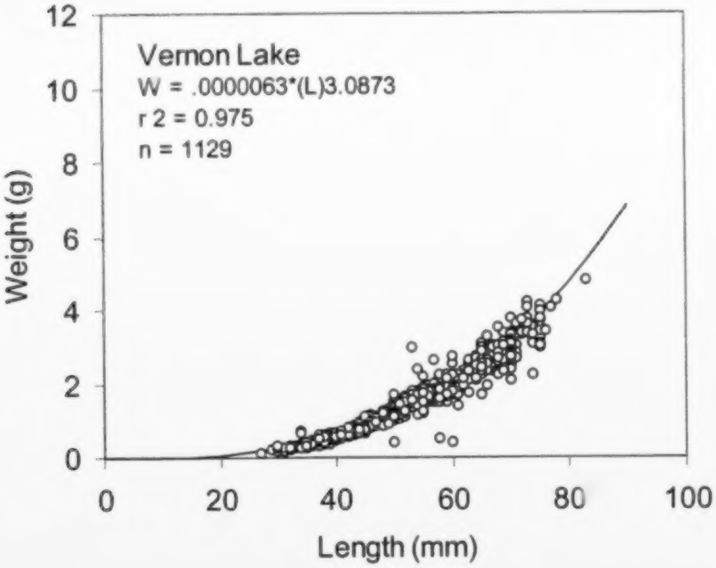


Figure 35. Vernon Lake juvenile *O. nerka* length-weight regression. Includes all data from all years.

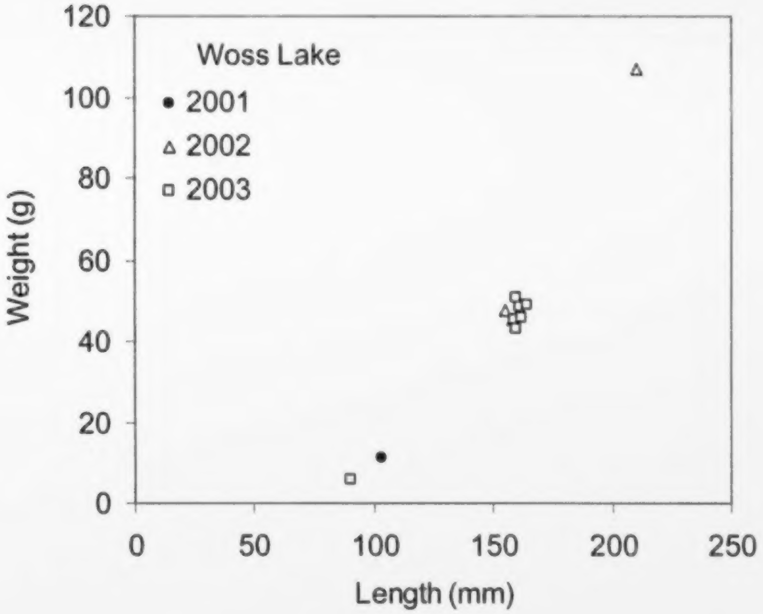


Figure 36. Woss Lake large *O. nerka* length-weights. The plots include all data from each year. Fish with lengths greater than 80 mm are assumed to be kokanee.

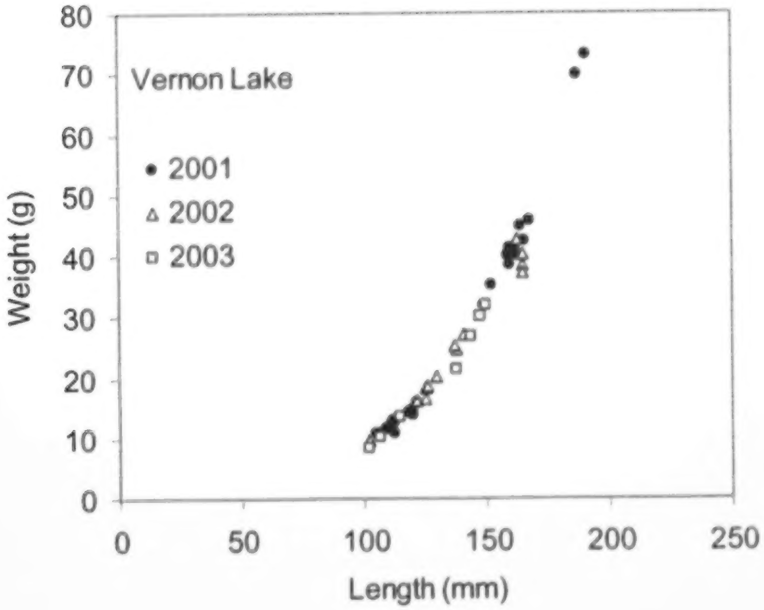


Figure 37. Vernon Lake large *O. nerka* length-weights. The plots include all data from each year. Fish with lengths greater than 80 mm are assumed to be kokanee.

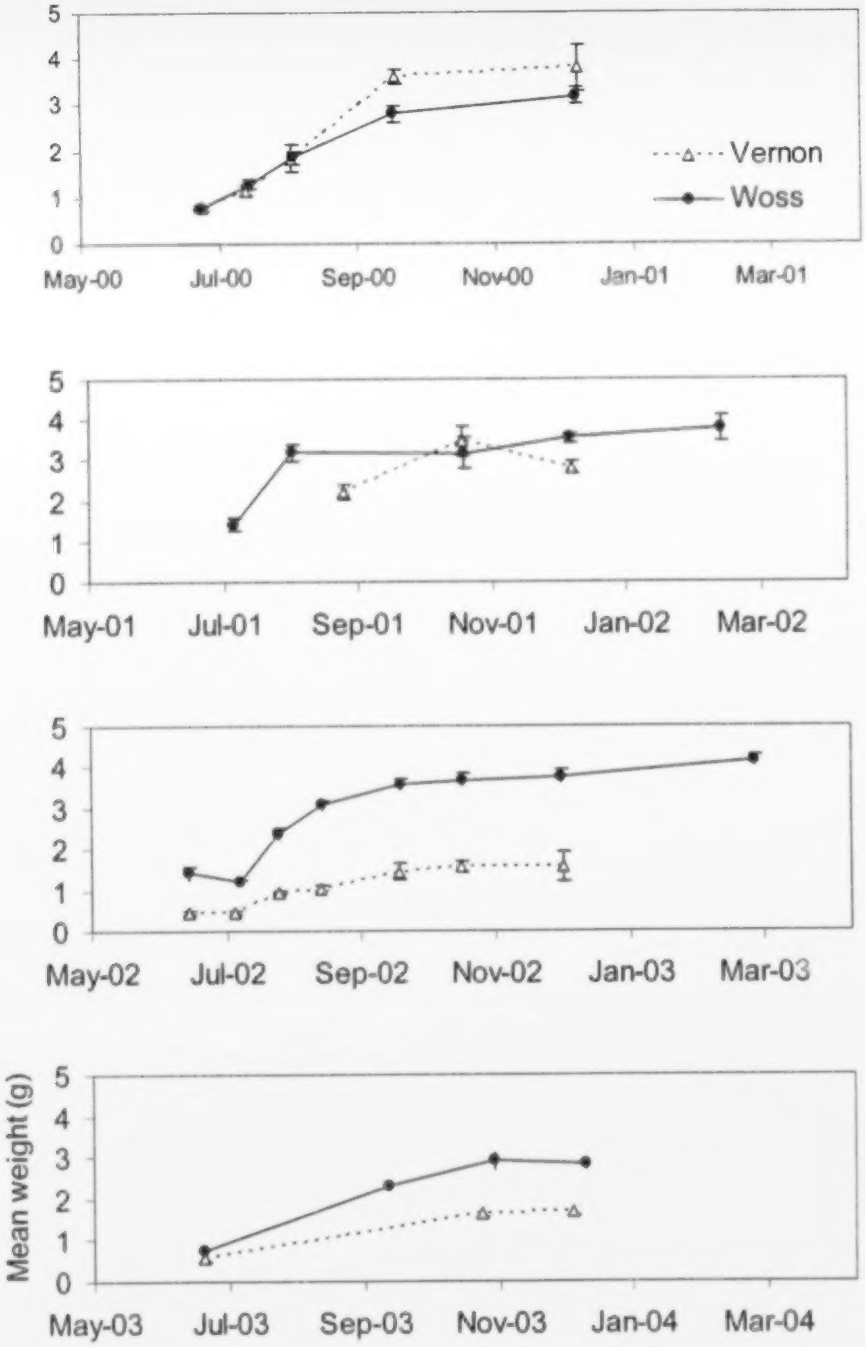


Figure 38. Year 2000-03 Woss and Vernon Lake juvenile sockeye weight (g) (± 95% confidence interval).

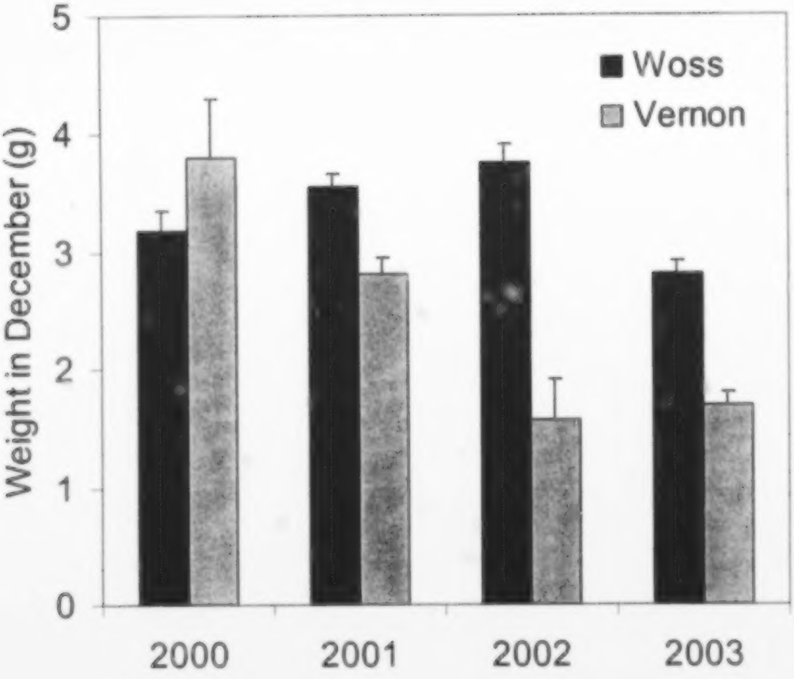


Figure 39. Woss and Vernon Lake juvenile sockeye weight (g) (± 95% confidence interval). For each year, values shown are only for the month of December.

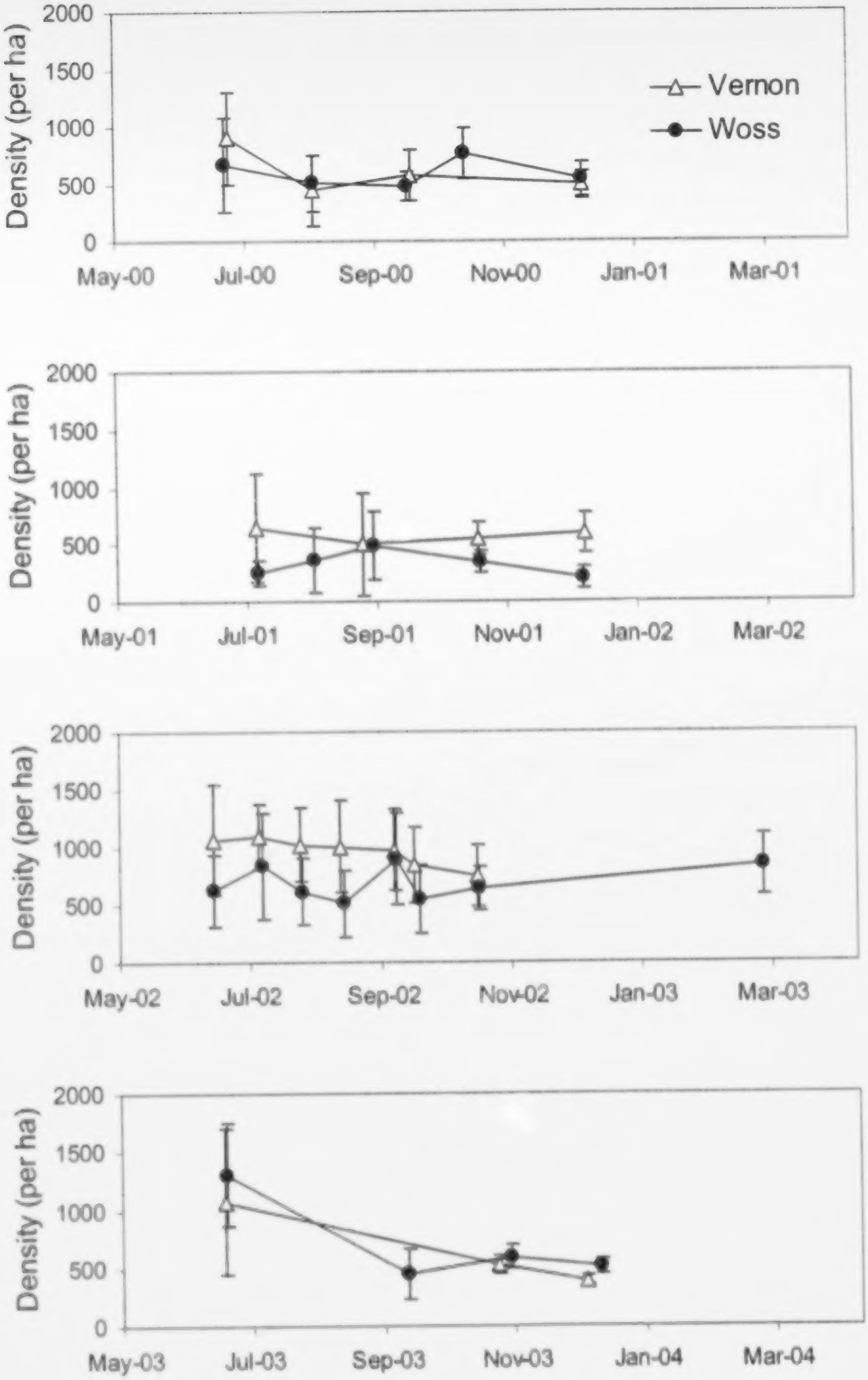


Figure 40. Year 2000-03 Woss and Vernon Lake juvenile sockeye population density (per ha) (± 95% confidence interval).

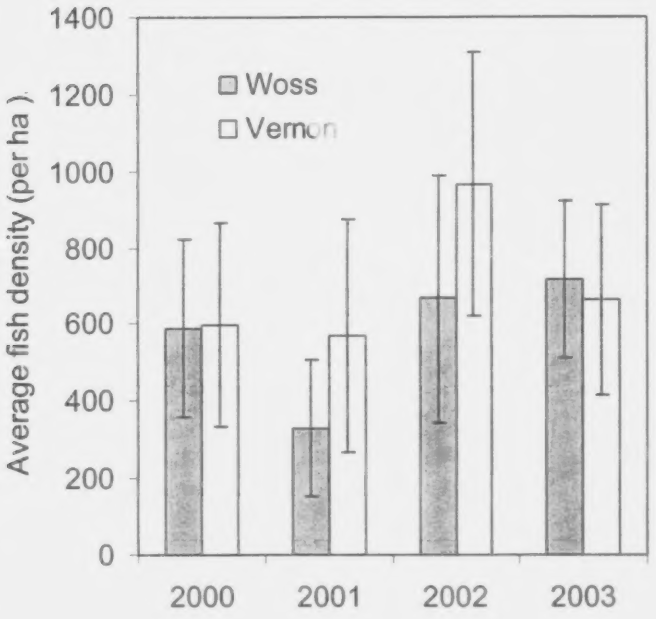


Figure 41. Year 2000-03 Woss and Vernon Lake mean annual juvenile sockeye population density (per ha) (± 95% confidence interval).

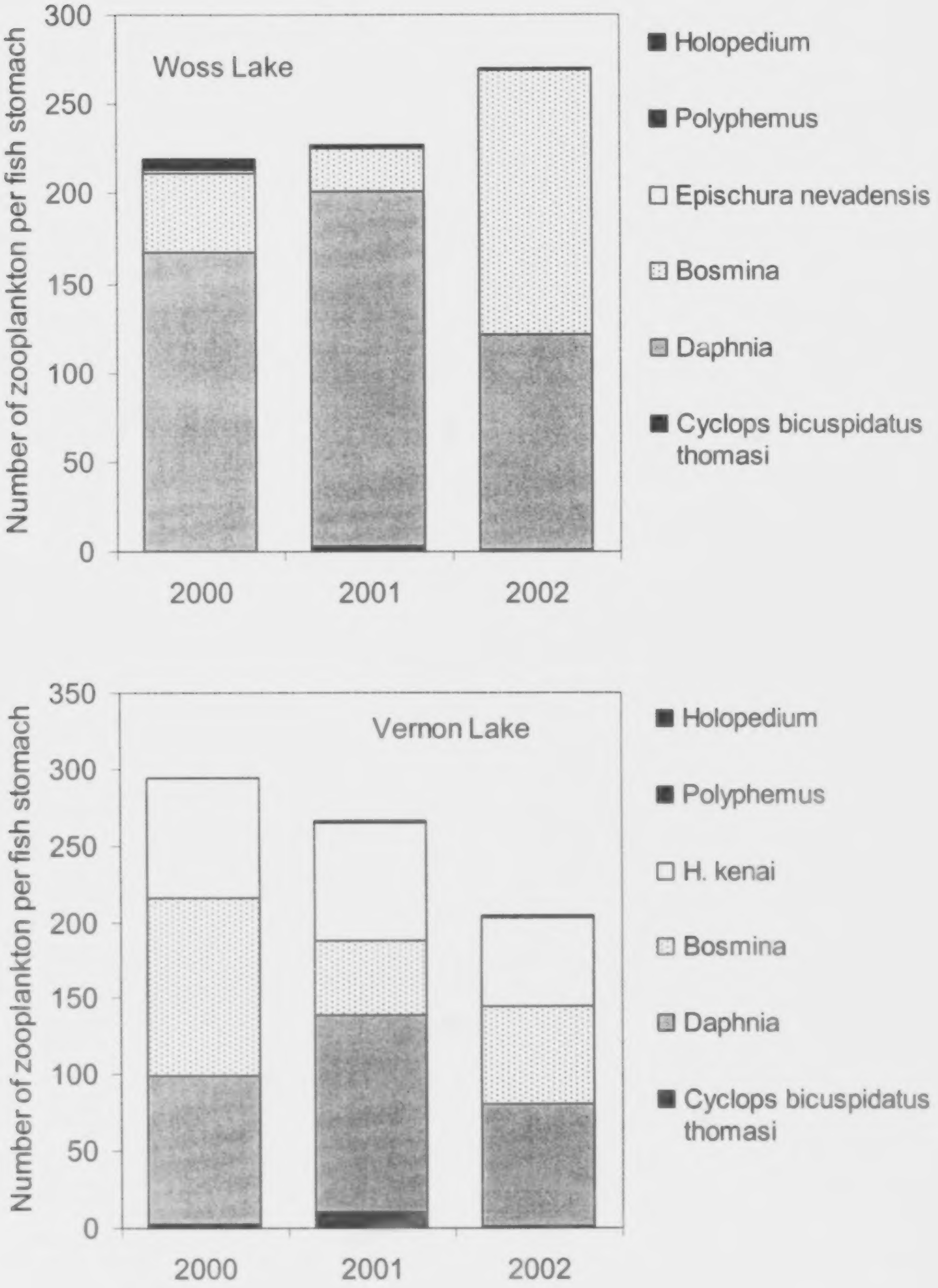
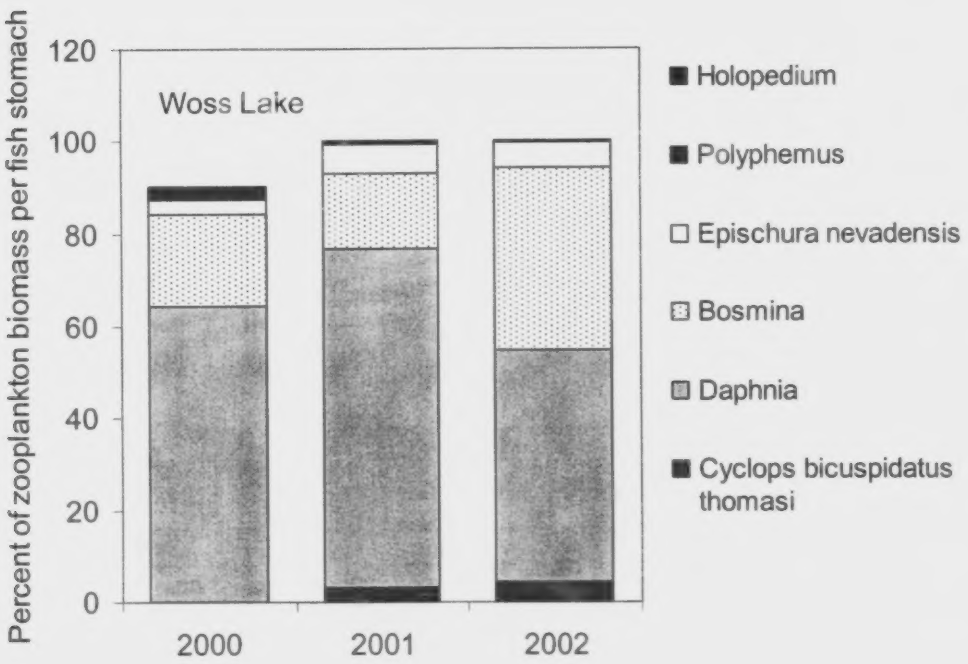


Figure 42. Average number of zooplankton prey found in each sockeye stomach. Detailed data are in table 25.



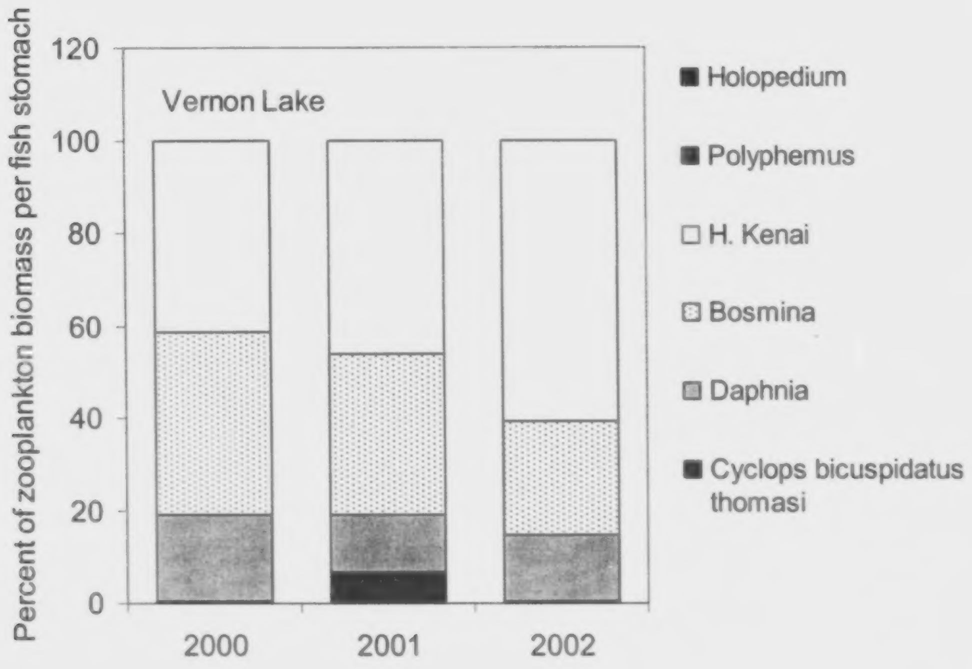
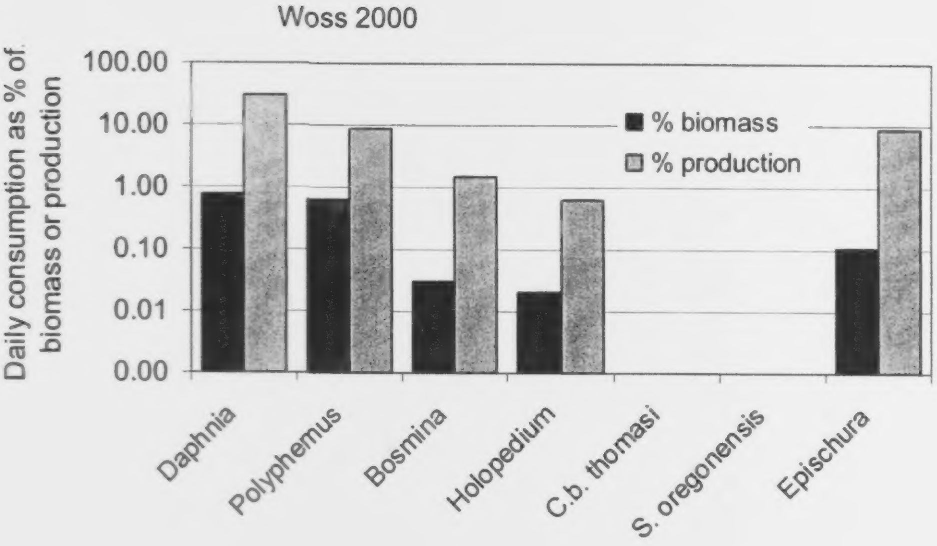


Figure 43. Percent zooplankton prey found in each sockeye stomach. Detailed data are in table 25.



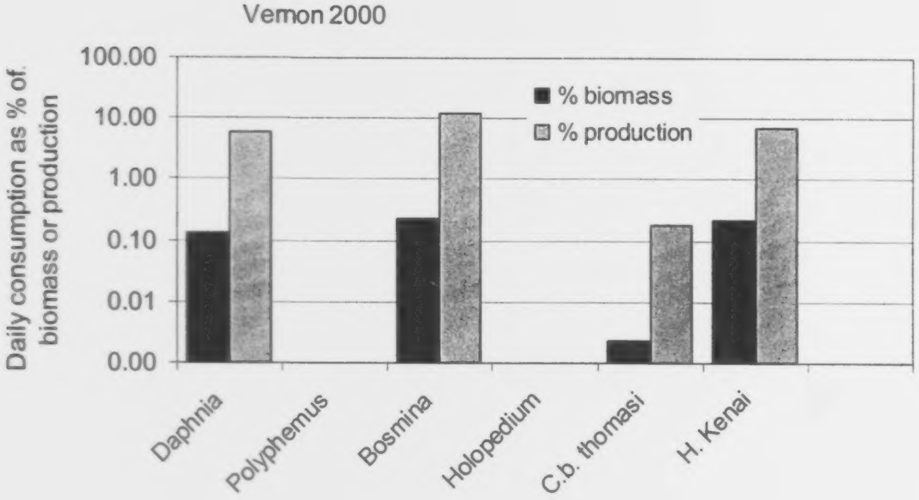
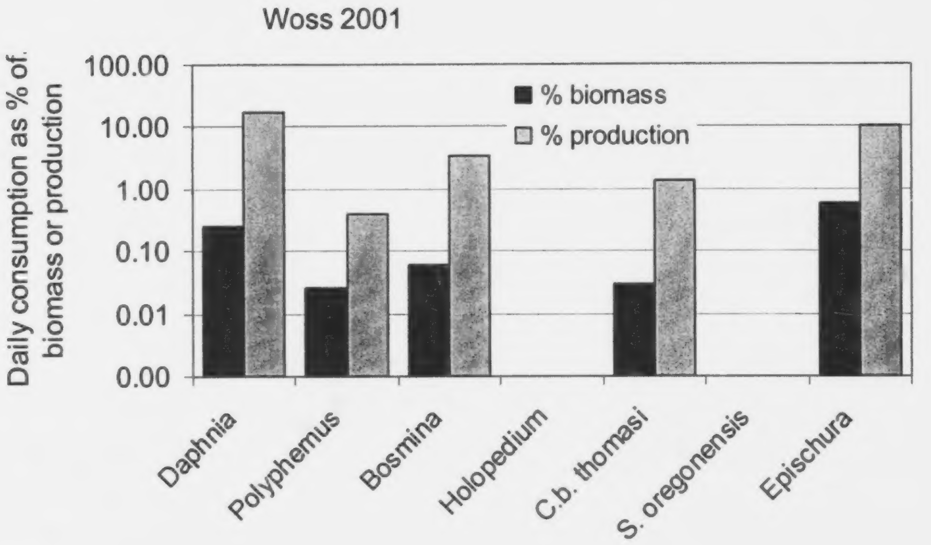


Figure 44. Year 2000 Woss and Vernon Lake; daily zooplankton consumption by fish, as a percentage of mean zooplankton standing stock (biomass) and mean daily zooplankton production.



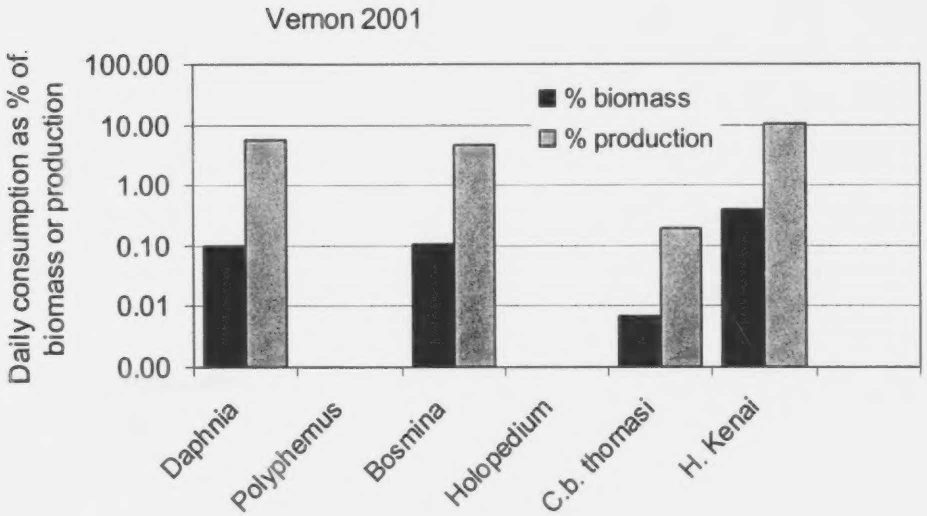


Figure 45. Year 2001 Woss and Vernon Lake; daily zooplankton consumption by fish, as a percentage of mean zooplankton standing stock (biomass) and mean daily zooplankton production.

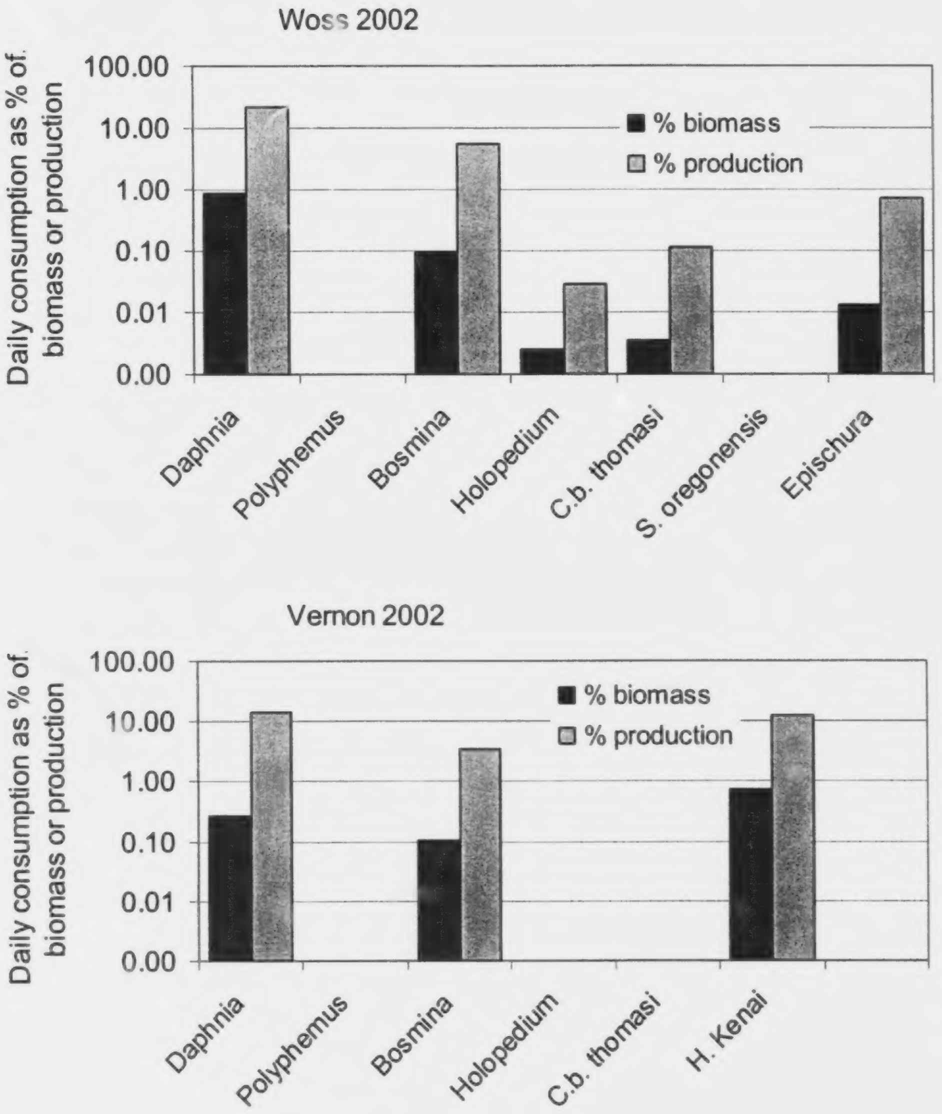


Figure 46. Year 2002 Woss and Vernon Lake; daily zooplankton consumption by fish, as a percentage of mean zooplankton standing stock (biomass) and mean daily zooplankton production.

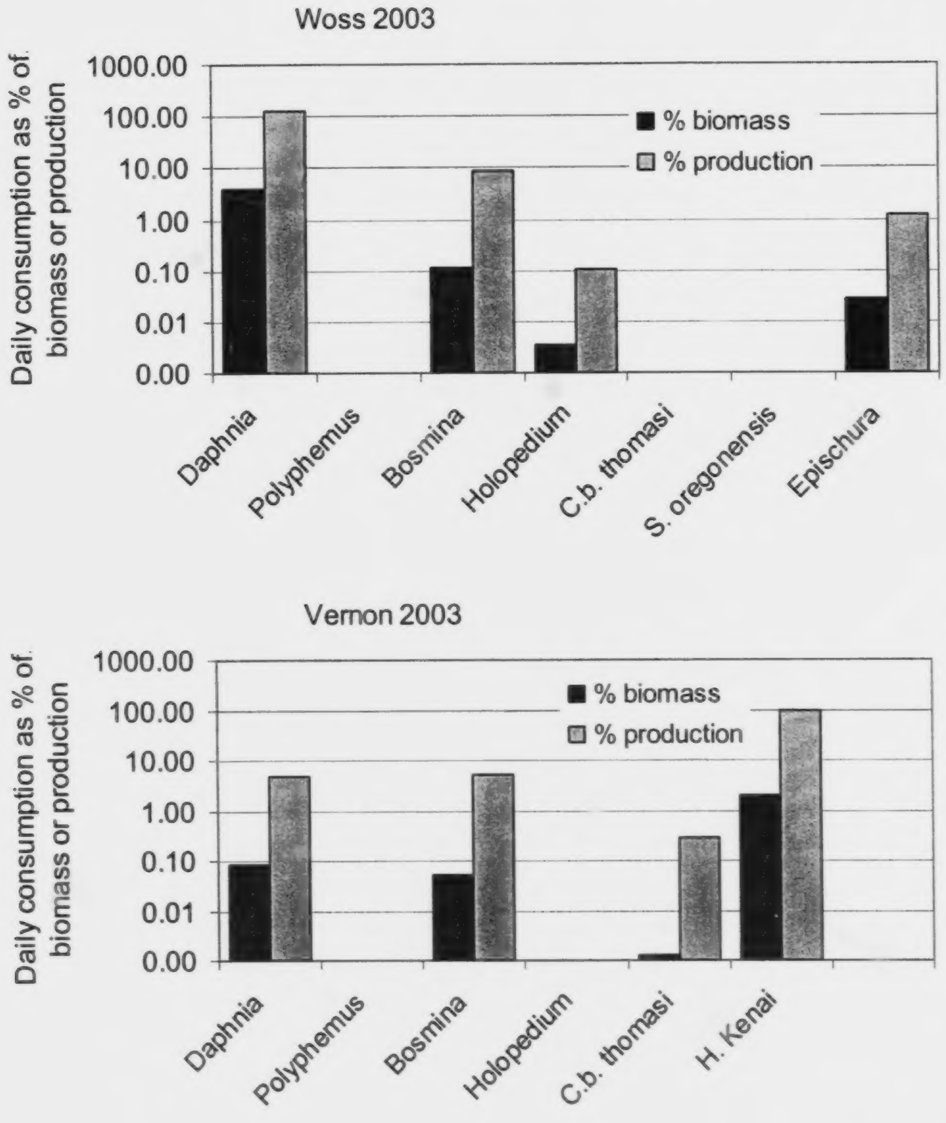


Figure 47. Year 2003 Woss and Vernon Lake; daily zooplankton consumption by fish, as a percentage of mean zooplankton standing stock (biomass) and mean daily zooplankton production. Note that axis has been expanded to accommodate consumption rates > 100% of production.

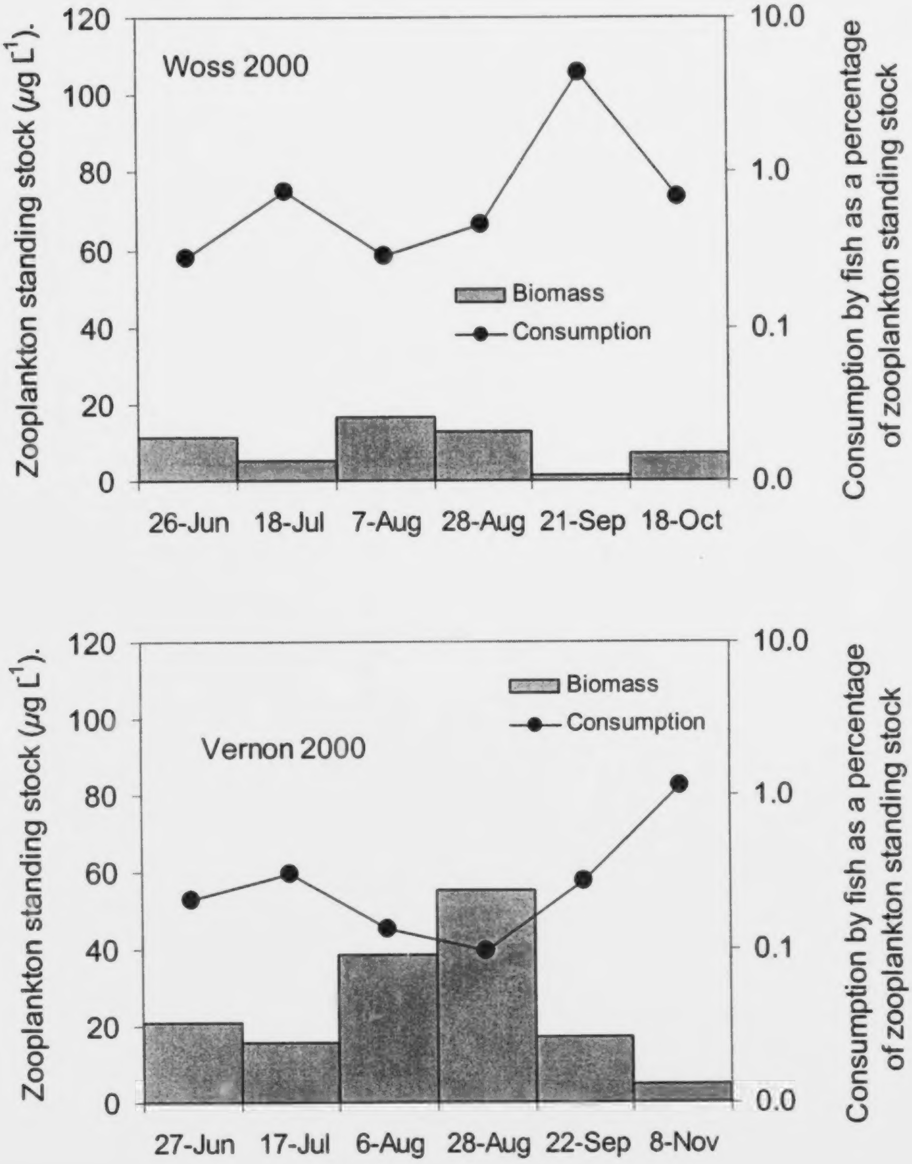


Figure 48. Year 2000 Woss and Vernon Lake edible zooplankton standing stocks (left axis) and daily consumption rates by fish as a percentage of zooplankton standing stock biomass.

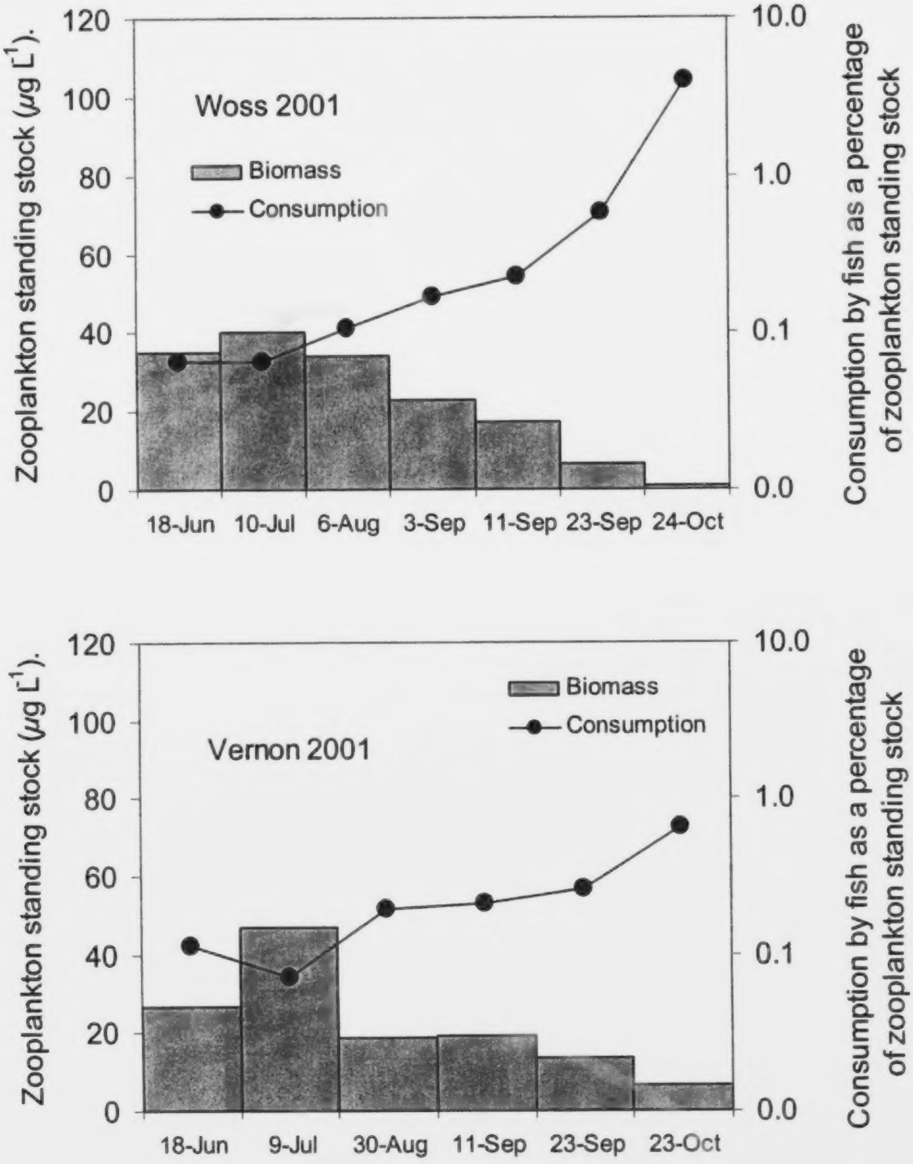


Figure 49. Year 2001 Woss and Vernon Lake edible zooplankton standing stocks (left axis) and daily consumption rates by fish as a percentage of zooplankton standing stock biomass.

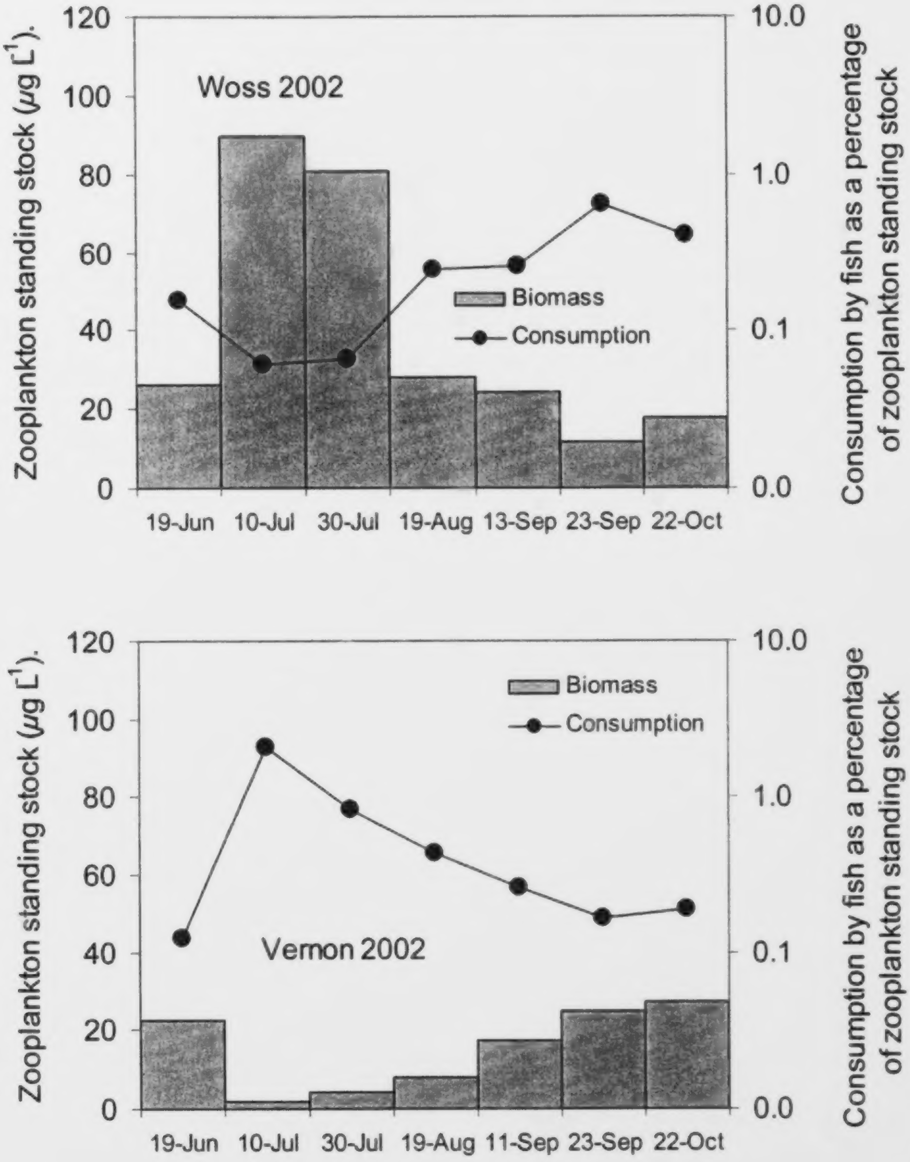
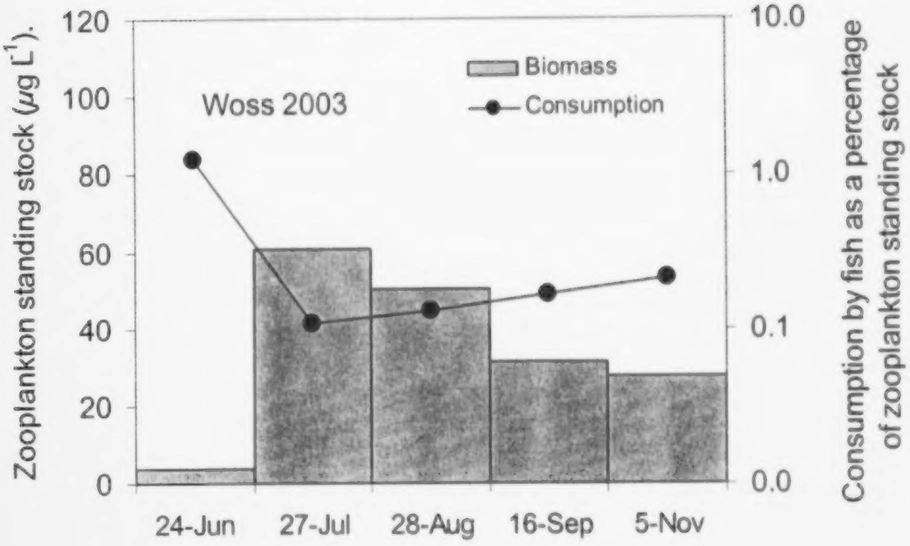


Figure 50. Year 2002 Woss and Vernon Lake edible zooplankton standing stocks (left axis) and daily consumption rates by fish as a percentage of zooplankton standing stock biomass.



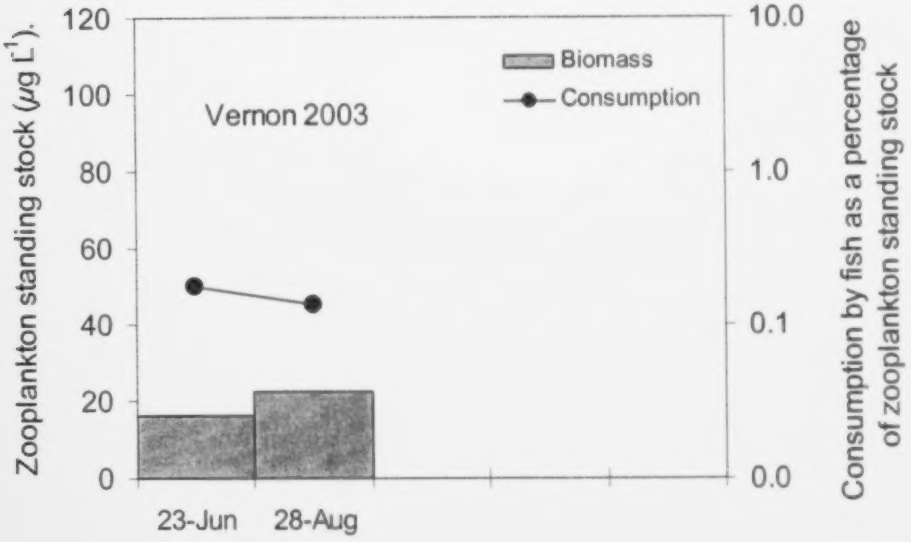


Figure 51. Year 2003 Woss and Vernon Lake edible zooplankton standing stocks (left axis) and daily consumption rates by fish as a percentage of zooplankton standing stock biomass.

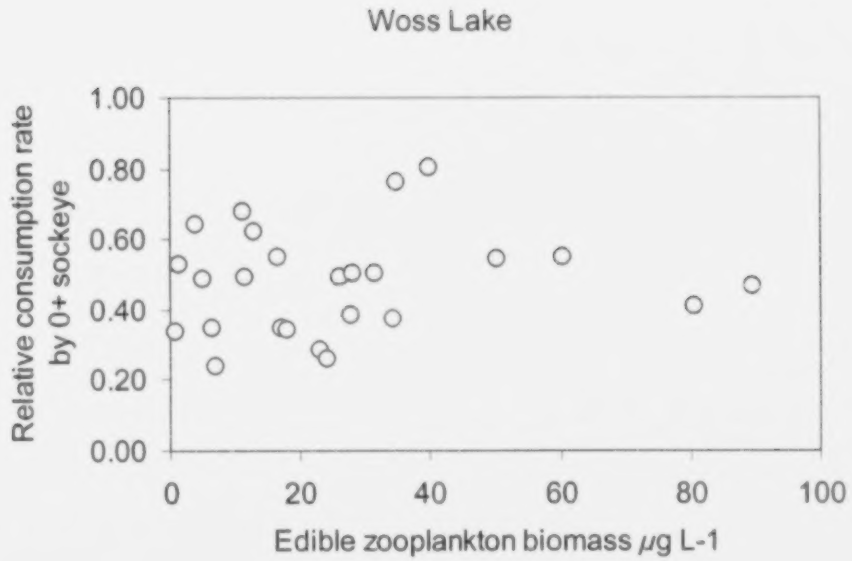


Figure 52. Year 2000-03, Woss Lake. Relative rates of daily consumption per unit biomass of 0+ sockeye biomass plotted with respect to edible zooplankton biomass. Relative rates = daily 0+ sockeye consumption ($\mu g\ L^{-1}\ d^{-1}$) divided by biomass ($g\ m^{-2}$) of 0+ sockeye measured on each consumption date.

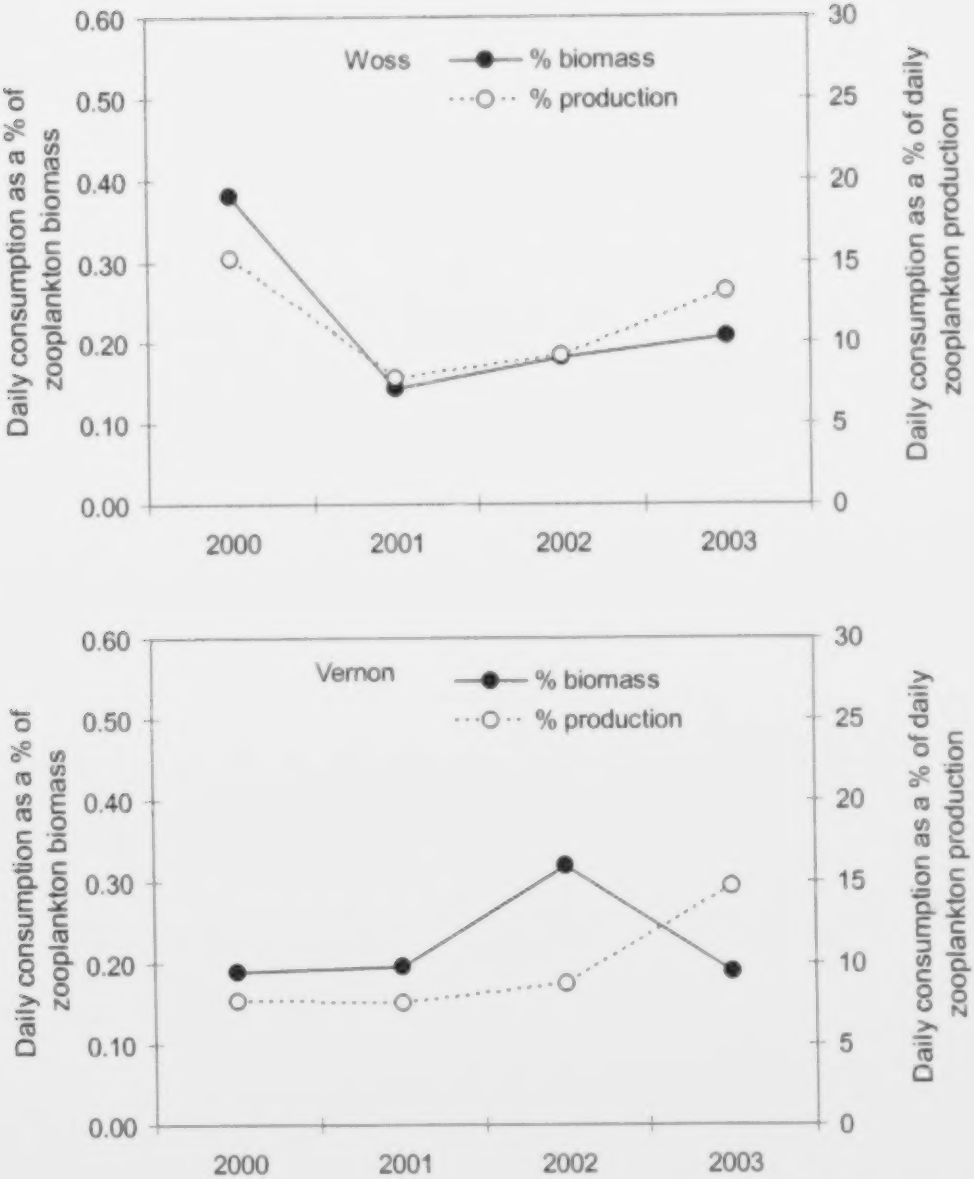


Figure 53. Mean annual daily consumption by 0+ sockeye as a percentage of zooplankton biomass (right) and mean daily zooplankton production (left).

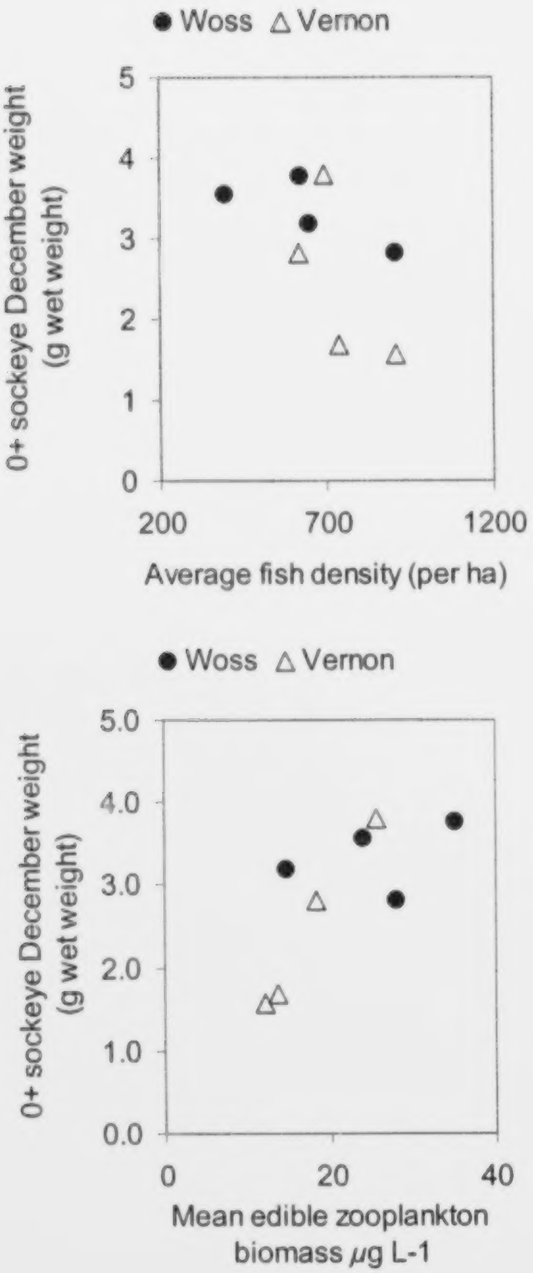


Figure 54. Top panel: Relationship between mean 0+ sockeye weight (g ww) in December and mean annual fish density. Bottom panel: Relationship between mean 0+ sockeye weight (g ww) in December and mean edible zooplankton biomass.

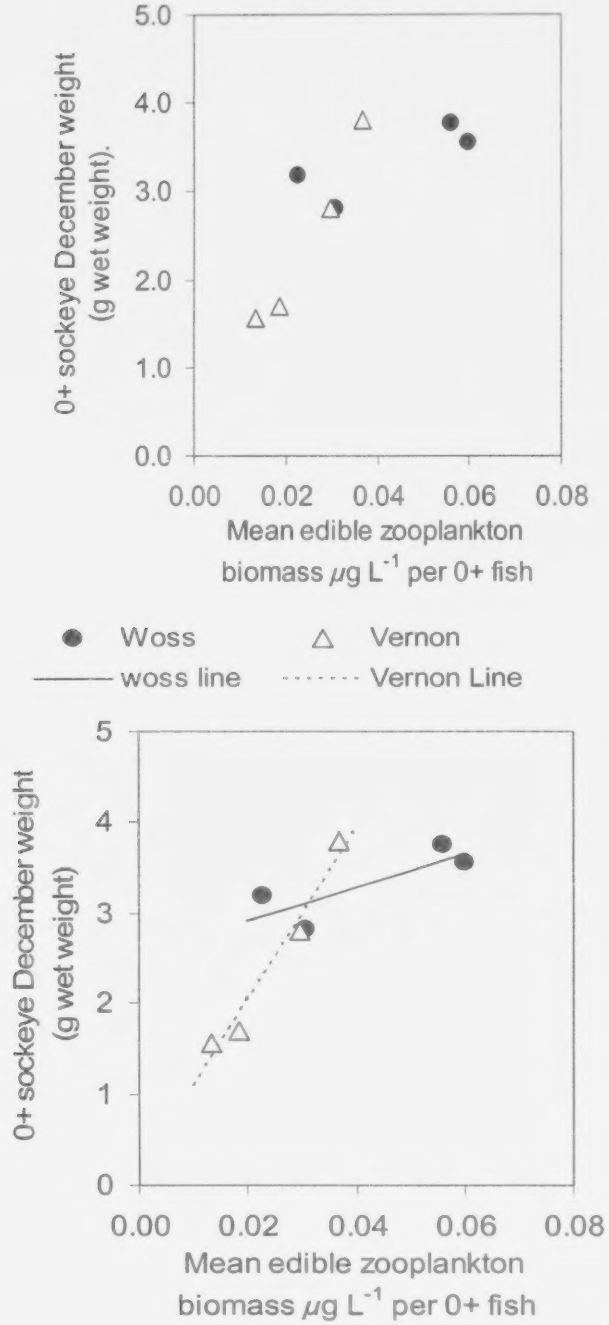


Figure 55. Top panel: Relationship between mean 0+ sockeye weight (g ww) in December and mean edible zooplankton biomass per fish. Bottom panel: Relationship between mean 0+ sockeye weight (g ww) in December and mean edible zooplankton biomass per fish. (Woss Lake correlation r = 0.53, p = 0.46) (Vernon Lake correlation r = 0.96, p = 0.037).

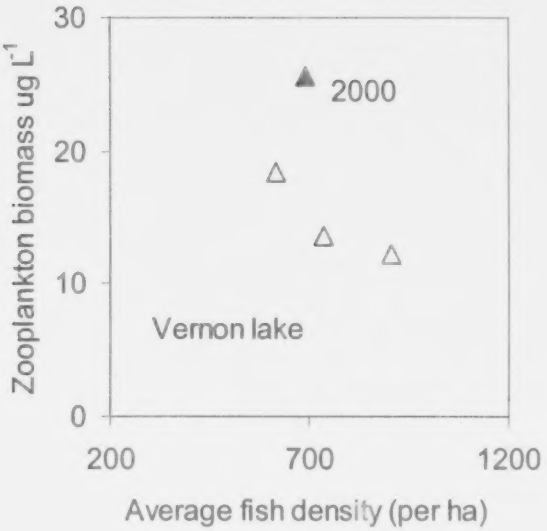


Figure 56. Vernon Lake, relationship between average zooplankton standing stock biomass and average fish density.

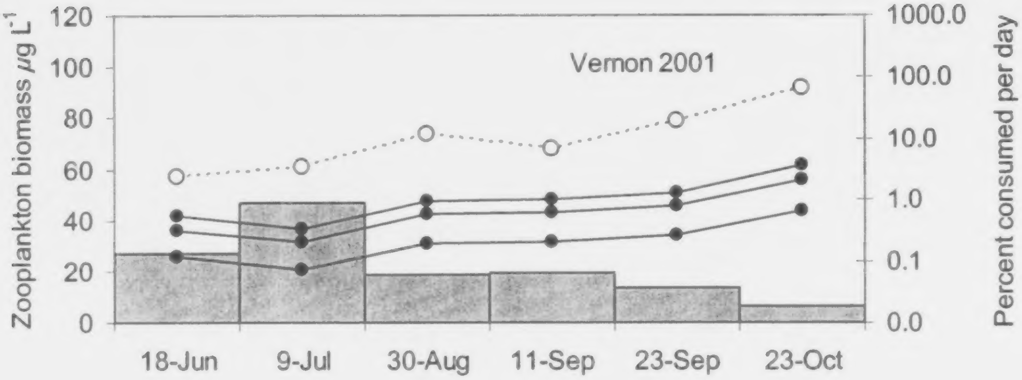


Figure 57. Year 2001 Vernon Lake edible zooplankton biomass (bars) and daily zooplankton consumption by fish as a percentage of mean zooplankton standing stock biomass (solid line and symbol) and mean daily zooplankton production (dotted line and open symbol). The two additional % biomass consumption lines, are for *O. nerka* populations comprising 85 % 0+ sockeye and 15 % kokanee and 70 % 0+ sockeye and 30 % kokanee.

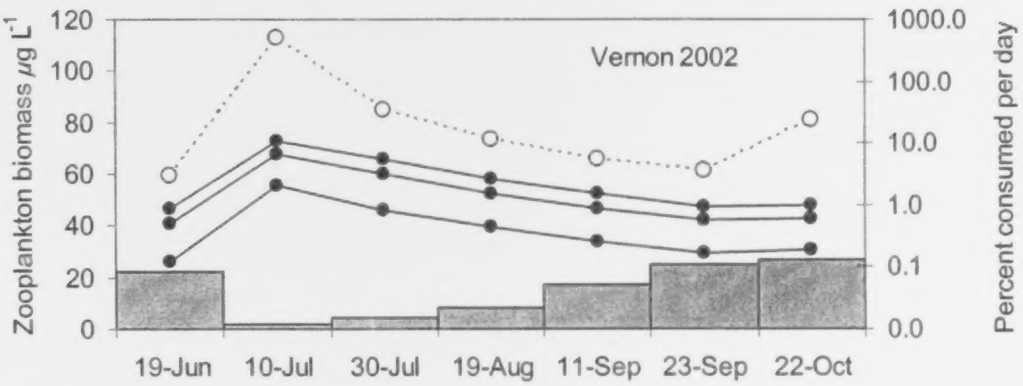


Figure 58. Year 2002 Vernon Lake edible zooplankton biomass (bars) and daily zooplankton consumption by fish as a percentage of mean zooplankton standing stock biomass (solid line and symbol) and mean daily zooplankton production (dotted line and open symbol). The two additional % biomass consumption lines, are for *O. nerka* populations comprising 85 % 0+ sockeye and 15 % kokanee and 70 % 0+ sockeye and 30 % kokanee.

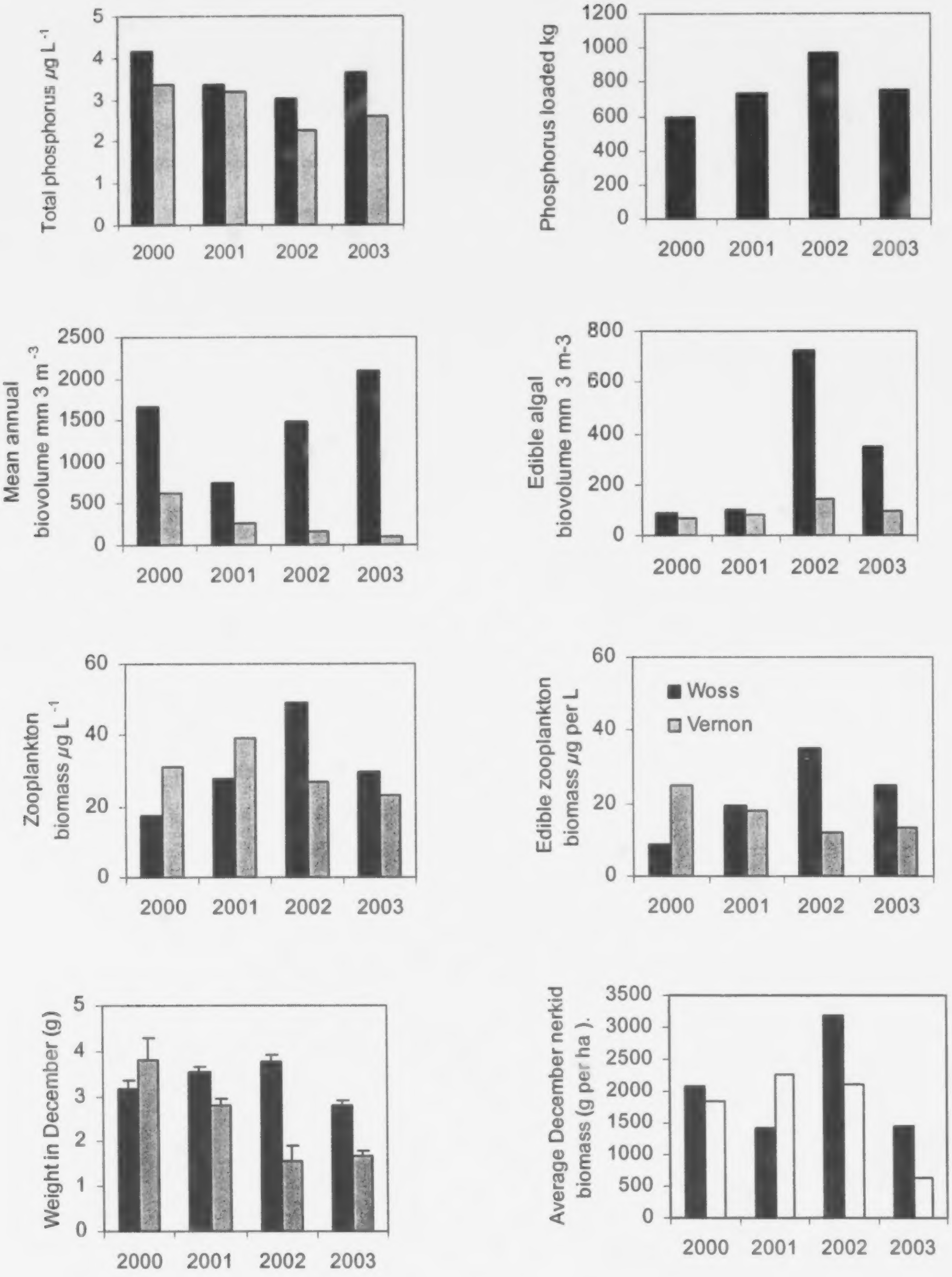


Figure 59. Mean annual (May - October) summaries for: Top row - epilimnetic phosphorus, and phosphorus loading in fertilizers. Second row - mean annual phytoplankton biovolume, and mean annual edible phytoplankton biovolume. Third row - Mean annual total zooplankton biovolume and edible zooplankton biovolume. Bottom row: Mean 0+ sockeye weight (± 95% confidence interval) and 0+ sockeye biomass.

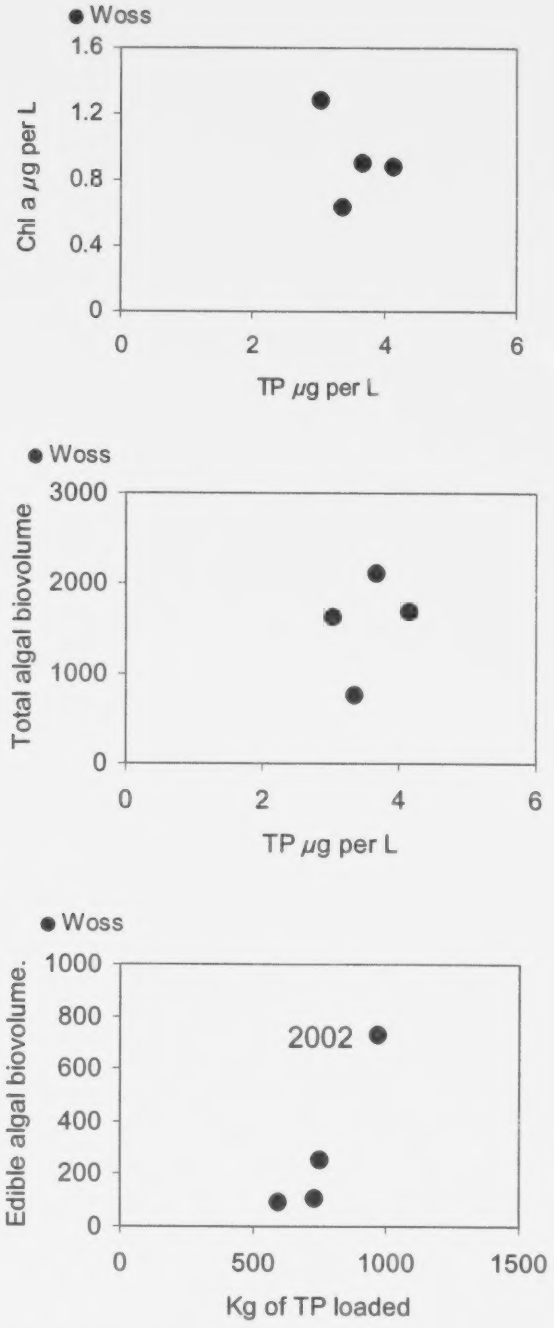


Figure 60. Woss Lake scatter plots for: Top - mean annual chlorophyll a with respect to mean annual epilimnetic TP. Middle - mean annual total algal biovolume (mm^3 m^{-3}) with respect to mean annual epilimnetic TP. Bottom - mean annual edible algal biovolume with respect to kg of TP added to the lake.

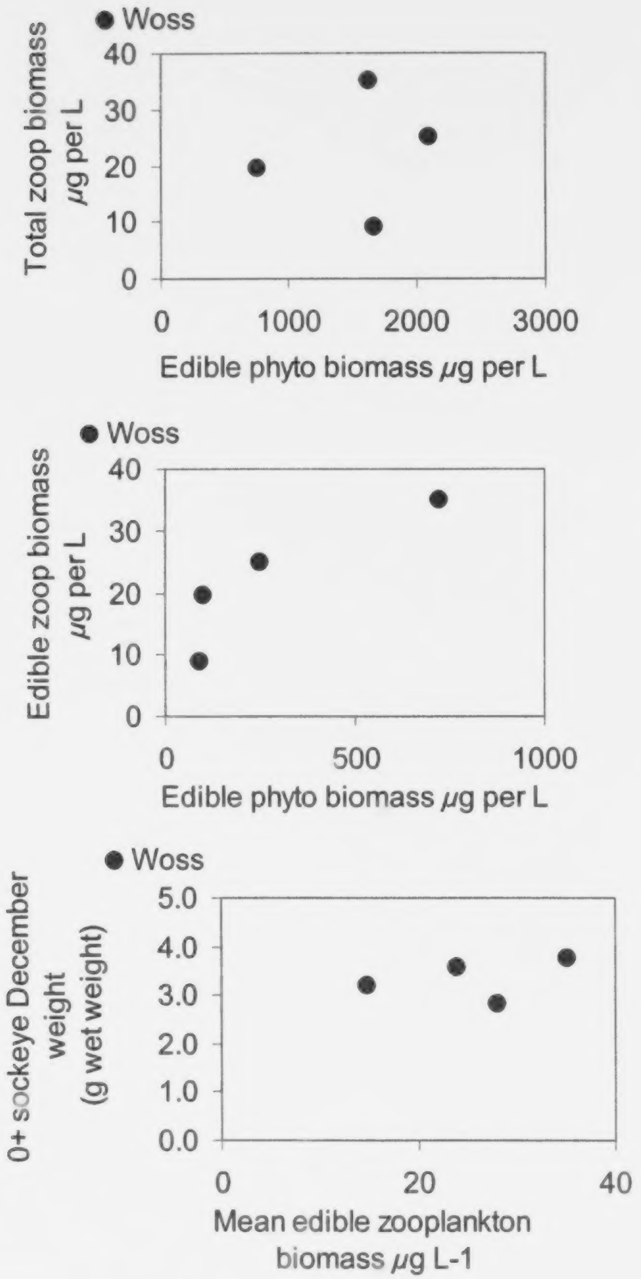


Figure 61. Woss Lake scatter plots for: Top - Mean annual total zooplankton biomass with respect to total phytoplankton biomass. Middle - Mean annual edible zooplankton biomass with respect to edible phytoplankton biomass. Bottom - Average 0+ sockeye weight in December with respect to mean annual edible zooplankton biomass.

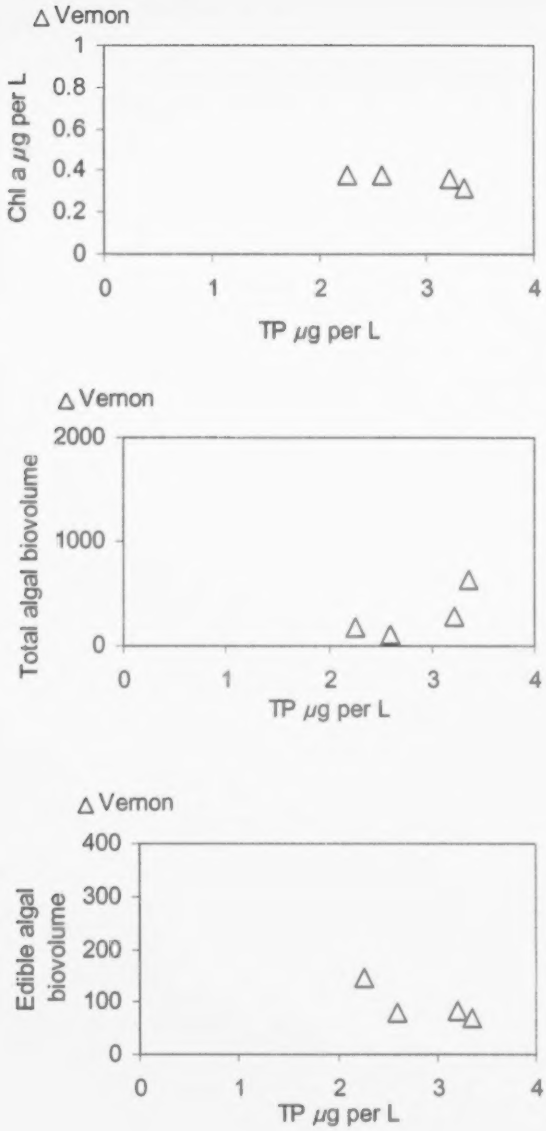


Figure 62. Vernon Lake scatter plots for: Top - mean annual chlorophyll a with respect to mean annual epilimnetic TP. Middle - mean annual total algal biovolume (mm^3 m^{-3}) with respect to mean annual epilimnetic TP. Bottom - mean annual edible algal biovolume with respect to epilimnetic TP.

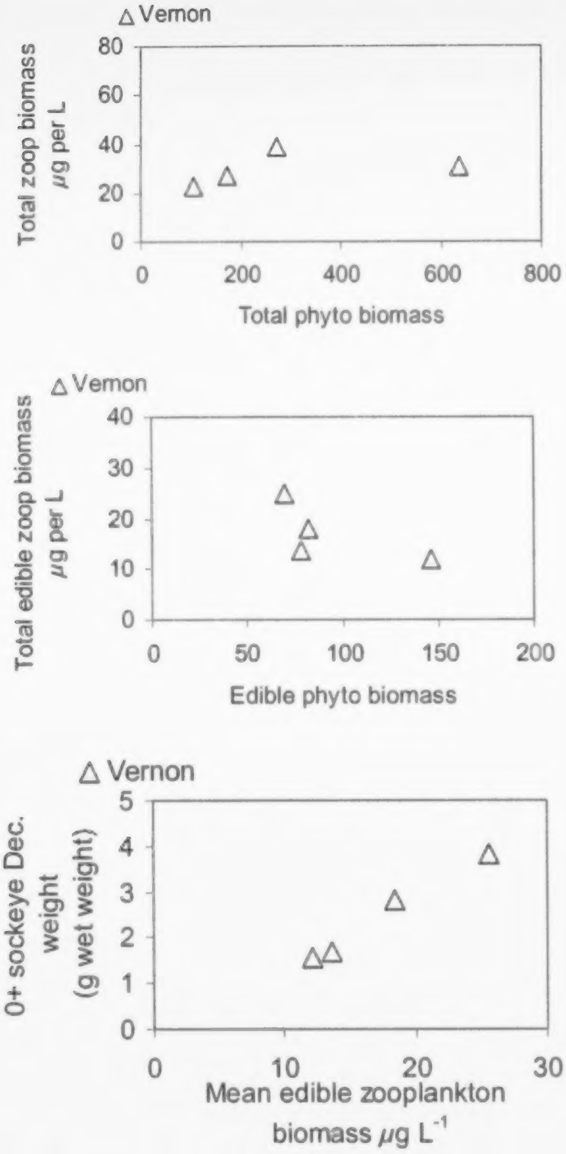


Figure 63. Vernon Lake scatter plots for: Top - Mean annual total zooplankton biomass with respect to total phytoplankton biomass. Middle - Mean annual edible zooplankton biomass with respect to edible phytoplankton biomass. Bottom - Average 0+ sockeye weight in December with respect to mean annual edible zooplankton biomass per fish.

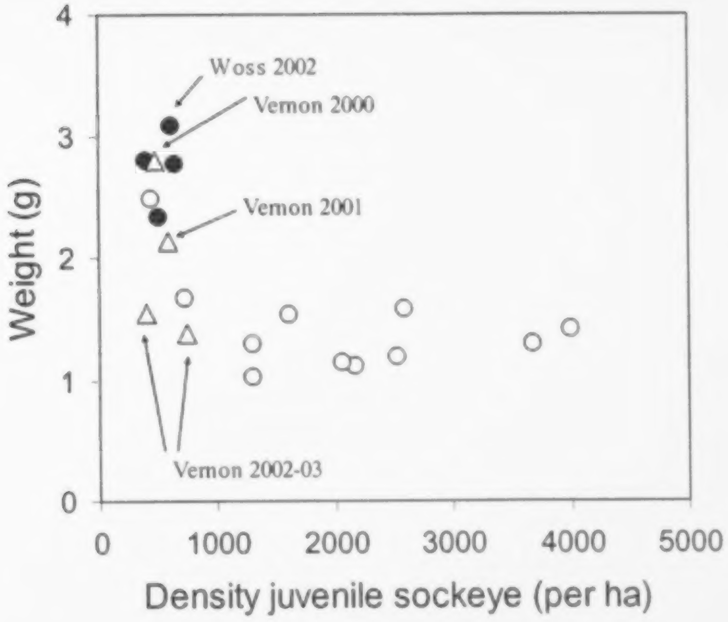


Figure 64. Sockeye fall-fry weights (g ww) with respect to density. The open circles are from Woss Lake surveys taken during 1978-96 . The closed circles are from Woss Lake surveys from 2000-03. The triangles are from Vernon Lake surveys from 2000-03.